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SCALE AND INTENSITY OF INTERTIDAL HABITAT USE BY KNOTS *CALIDRIS CANUTUS* IN THE WESTERN WADDEN SEA IN RELATION TO FOOD, FRIENDS AND FOES

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ABSTRACT

In August-October 1988-1992 we studied the distribution and abundance of knots *Calidris canutus* around Griend in the western Wadden Sea, and the extent to which these can be explained by benthic prey availability and presence of avian predators. Numbers in the nonbreeding season showed monthly averages of 10000 to 25000 birds. Over 100000 knots were recorded on three occasions. Knots feed in large flocks, individual birds usually experiencing 4000 to 15000 flock-mates. The Siberian-breeding/west-African wintering *canutus* subspecies passed through in late July and early August. Otherwise the Greenlandic/Canadian breeding *islandica* subspecies was present. Over the period 1964-1992 there were no clear trends in the number of knots, but *canutus*-knots were particularly abundant in July-August 1991, whereas in 1992 both subspecies were absent.

***Macoma balthica* was the preferred prey of both subspecies. *Hydrobia ulvae*, *Mytilus edulis* and *Cerastoderma edule* were eaten when *Macoma* was absent close to the surface of the sediment. As *Macoma* buried deeper from July onwards, *canutus* faced better average feeding conditions than *islandica* later in the year. The spatial distribution of knots feeding on the intertidal flats around Griend was best explained by the harvestable biomass of the prevalent prey species in a particular year and season, *i.e. Macoma* (main prey when their harvestable biomass densities were greater than *ca* 0.8 g AFDM per m^2) and *Cerastoderma*, and by the avoidance of situations where they run the risk of attack by bird-eating birds. Flocks of knots covered most of the intertidal flats in the western Dutch Wadden Sea in a couple of tidal cycles. This is about 800 km^2, much larger than the equivalent area used by knots on their wintering grounds in Mauritania (10-15 km^2), a difference that is correlated with prey spectrum, prey availability and predictability.**

1. INTRODUCTION

A central theme in animal ecology is the explanation of distribution and abundance (ELTON, 1927; ANDREWARTHA & BIRCH, 1954; KREBS, 1972). Food provides the most obvious critical resource, and many studies have been devoted to correlating distribution of animals with their food resources. Nonbreeding shorebirds provide a good system for such studies because they usually occur highly visible in open habitats and since their feeding behaviour and the availability of their food are relatively easy to quantify. The quality of different feeding habitats can be directly measured in studies on food selection and intake rates (*e.g.* GOSS-CUSTARD, 1984), and the distribution patterns of shorebirds explained accordingly (GOSS-CUSTARD, 1970a; ZWARTS, 1974; HULSCHER, 1982; ZWARTS *et al.*, 1992). More indirect evaluations of food-and-feeding constraints on habitat choice come from comparisons of patterns in food availability and shorebird abundance over time scales of a tidal cycle (*e.g.* BURGER *et al.*, 1977; CONNORS *et al.*, 1981), periods longer than a week (CONNORS *et al.*, 1981; GOSS-CUSTARD, 1983), between years (ZWARTS *et al.*, 1992) and between areas (GOSS-CUSTARD, 1970b; GOSS-CUSTARD *et al.*, 1977b, 1991; BRYANT, 1979; HICKLIN & SMITH, 1984; WILSON, 1990; ZWARTS *et al.*, 1990; COLWELL & LANDRUM, 1993). In these kinds of analyses, independent interfering variables may blur relevant correlations, and there is a problem in assigning causality. Nevertheless, the correlative approaches do allow the definition of the temporal and spatial scales over which shorebirds choose their feeding area.

Shorebirds lend themselves well to interspecific comparative studies (*cf.* CLUTTON-BROCK & HARVEY, 1984) on scale-effects of food exploitation, since they

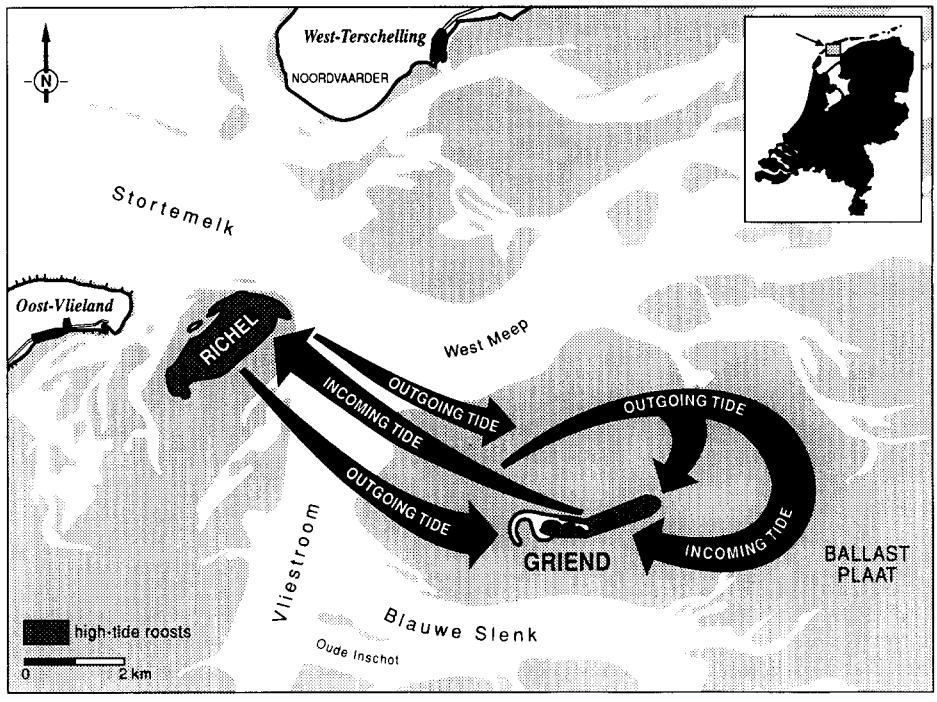


Fig. 1. An overview of the study area in the western Wadden Sea, The Netherlands and a summary of the typical tidal movements of knots during incoming and outgoing tides. The intertidal area indicated by shading is bordered by the mean low-water mark at spring lows.

show great variation in food-and-feeding related distribution patterns. GOSS-CUSTARD (1970a) and MYERS (1984) have capitalized on this in their analyses of the spacing behaviour of nonbreeding shorebirds. However, as emphasized by MYERS (1984), the descriptive basis for such comparative studies is yet small, and this has not changed much since the early eighties. One large and abundant species which is easy to study, the oystercatcher *Haematopus ostralegus*, has had a disproportionate share of the attention. Oystercatcher-distributions appear strongly shaped by processes of interference, dominance and territoriality (GOSS-CUSTARD *et al.*, 1982, 1984; SUTHERLAND & KOENE, 1982; ENS & GOSS-CUSTARD, 1984), with a tendency for individual birds to confine their low-water movements to areas less than one ha. This is in stark contrast with the feeding and spacing behaviour of a flocking and wide-ranging species such as the knot *Calidris canutus* (PRATER, 1972). In this species, single flocks (which number up to 30000 birds) roam over areas as large as 30 km^2 in the course of a single low-water period.

Knots are characterized by long seasonal migrations between the high-arctic breeding grounds and the nonbreeding areas, always using coastal intertidal habitats at temperate or tropical latitudes (PIERSMA & DAVIDSON, 1992). Knots usually feed on molluscs which are ingested whole. This means that their faeces can yield accurate information on diet (DEKINGA & PIERSMA, 1993). Two subspecies of knots occur in the Wadden Sea, where this study took place. In the periods July-August and May members of the Afro-Siberian subspecies *canutus*, which breeds in Siberia, use the area as a refuelling site on their way to and from the west African wintering grounds (PIERSMA *et al.*, 1992). From August to April large numbers of the subspecies *islandica* occur in the Wadden Sea, which thus provides an important moulting and wintering area (DAVIDSON & WILSON, 1992). Over the summer small numbers of knots remain in the Wadden Sea (BOERE & SMIT, 1983), presumably of the subspecies *islandica* as nonbreeding *canutus* are likely to remain in West Africa (VAN DIJK *et al.*, 1990).

Our study, based on five seasons of fieldwork on Griend in the western Dutch Wadden Sea, supplements the pioneering work of PRATER (1972), GOSS-CUSTARD (1977) and GOSS-CUSTARD *et al.* (1977a), and recent studies on the food and feeding of knots on staging areas in Iceland (ALERSTAM *et al.*, 1992) and in the Dutch Wadden Sea (ZWARTS & BLOMERT, 1992; ZWARTS *et al.*, 1992). We describe the seasonal occurrence of knots, identify when the two populations occur in the area, describe their diet and the abundance of their prey, and the use of different feeding areas in different years. We try to explain the spatial occurrence of feeding and roosting knots from the availability of food and the putative safety from predators, *e.g.* by correlating bird abundance with food

availability among areas and among years.

2. STUDY AREA

Griend is a small island, without a resident human population (53°14'N, 05°15'E; Fig. 1). What is left of Griend today are the rescued remains of a much larger island, historically known as Griend, Grint or Gryn since the early Middle Ages. Since then, Griend has continuously decreased in size, and would have turned into intertidal flat had humanity not intervened (BROUWER *et al.*, 1950; VEEN & VAN DE KAM, 1988). From, 1941 onwards, the western edge of Griend has repeatedly been enforced by various types of breakers and dikes. The last reconstruction was the largest, and was carried out during the very start of this study, in August-October, 1988. A 2.5-km long dike in the shape of a hockey-stick was built west and north of the old circular island. Griend thus increased in size from 0.16 to 0.35 km^2 (ESSINK & BOSCH, 1993). The central saltmarsh and creek system, often used by knots and other shorebirds as a high-tide roost (VEEN & VAN DE KAM, 1988), was left intact. The general public is not allowed on Griend, law being enforced during April-August by wardens/scientists living in a house on poles on the 'old island'.

In the direction of Vlieland, 7.5 km WNW of Griend, lies the nearest other island, Richel, which is a low-lying barren sandflat covering 2.4 km^2. Some species (notably knot, grey plover *Pluvialis squatarola* and curlew *Numenius arquata*), feeding on the intertidal flats around Griend, often use Richel as an alternative high-tide roost, especially during spring tides (see Fig. 7). A general impression of the movements of knots during a tidal cycle when they roosted on Richel is given in Fig. 1.

The intertidal flats around Griend, varying in height between -30 cm and +80 cm above D.O.L. (Dutch Ordinance Level, the 'Nieuw Amsterdams Peil', which is close to the mean-tide level; Fig. 7), are exposed for 2 to 7 h per low-water period. Heights, and corresponding emersion times, are greatest east and

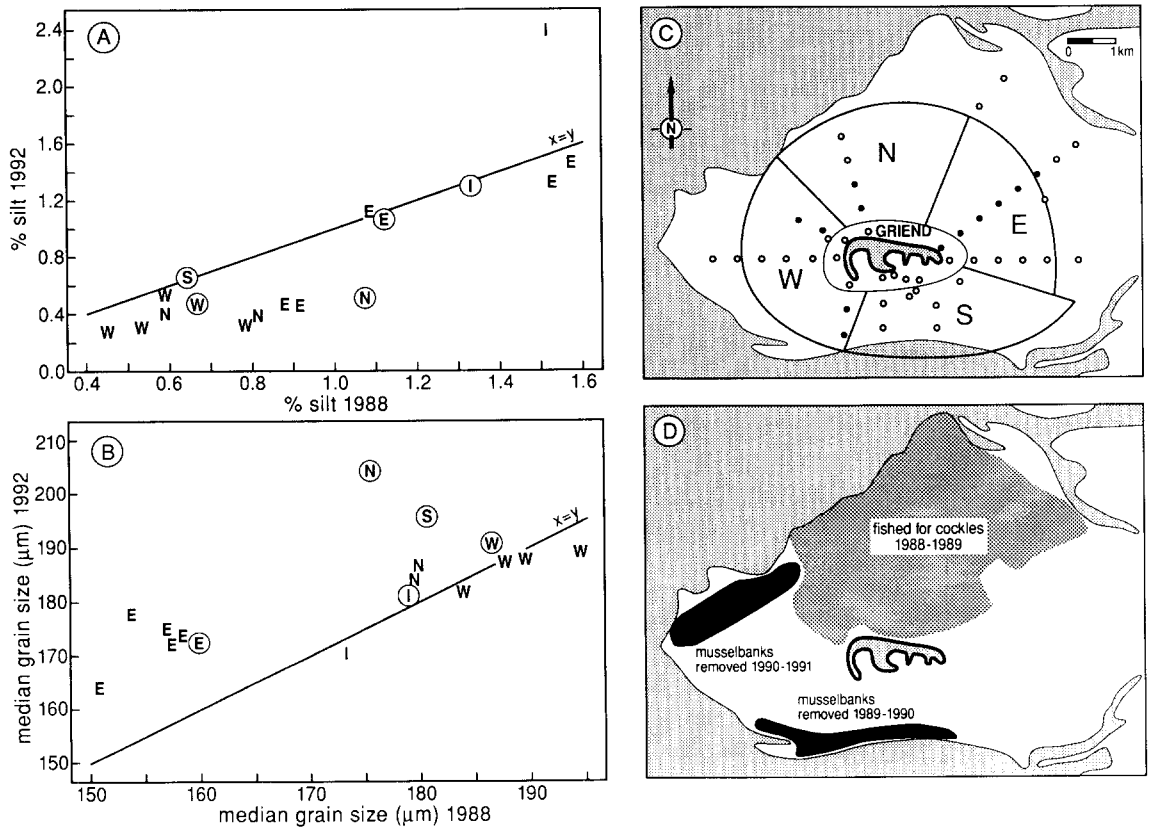


Fig. 2. Sediment related changes of the intertidal flats around Griend in the period 1988-1992. (A) gives a comparison of the silt content and (B) of grain size distribution (median grain size) of the intertidal sediments around Griend in 1988 and 1992. The map in (C) indicates the five sectors around the island as well as all the benthic sampling stations in 1988-1992. Filled dots indicate stations at which sediment samples were taken in both 1988 and 1992 (given in scattergrams A and B), the other sampling stations are shown by open circles. The area dredged for cockles in 1988-1989 and the extent of musselbanks removed in 1989-1991 are indicated in (D).

northeast of the island. The latter areas even remain dry during low high-water periods and are then used as a roost (see Fig. 7). With a silt content (defined here as the sediment-fraction not retrieved on a 50 μm mesh; see BARETTA-BEKKER *et al.*, 1992) which is always less than 1.5% (Fig. 2A), the intertidal flats around Griend can be characterized as sandy (*cf.* DANKERS & BEUKEMA, 1983). This is also reflected in the median grain-size values of 150-200 μm (Fig. 2B), which belong to the highest reported for the Wadden Sea by DANKERS & BEUKEMA (1983) and by ZWARTS (1988). A comparison between 1988 and 1992 (Fig. 2A, B) shows that the silt fraction has decreased in the western, northern and eastern sectors around the island, and that the median grain size has increased everywhere except in the east and north. In short, the intertidal flats have become more sandy, an effect which we attribute to the loss (Fig. 2D) of silt-producing and wave-breaking musselbeds (*Mytilus edulis*) in the northwest and southwest (this is the direction from where the winds are coming during storms), and the reworking of large areas of sediment during cockle (*Cerastoderma edule*) dredging in September-October, 1988 (PIERSMA *et al.*, 1993a).

3. METHODS

3.1. BIRD NUMBERS AND SUBSPECIFIC IDENTITY

Since 1964 the wardens of Griend have carried out high-water counts of all waterbirds roosting on and close to Griend at approximately weekly intervals in the period April-July. At irregular intervals supplementary counts were made by visiting parties outside the breeding season. The data collected between 1964 and 1987 have been summarized by VEEN & VAN DE KAM (1988) and are incorporated in the updated database used here.

From 1988 to 1992 knots were intensively studied in the period August-October, weather, logistics and volunteer effort permitting. Before 1988, when the island was small, the whole area exposed at high-tide could usually be surveyed from the wardens' house. This became impossible with the construction of the 2.5-km long dike, behind which much of the area and many roosting flocks disappeared from sight. Since then, knots and other waterbirds have been counted by two parties of 1-2 persons, one covering the west end and the other the eastern half of the island. At the start of the study in 1988, it became clear that at the higher high tides a lot of birds disappeared from Griend during high water, having first assembled on the high-lying sandflats northeast of Griend and then flying to Richel. Since this discovery, most counting parties took the effort to separately count the knots flying to Richel, but there is inconsistency in the methods here. We do not know whether the roost flights to Richel are a recent phenomenon coinciding with the building of the large dike, or whether knots and other shorebirds also flew onto Richel before 1988.

In order to estimate the number of knots departing on long-distance flights, we tried to keep an open ear and eye in the afternoons and evenings in August--September, especially when the setting sun was visible (see PIERSMA *et al.*, 1990). When a departing flock was noticed, usually calling loudly, we counted the number of birds and took an approximate bearing of the departure direction. Part of the knot data was presented by PIERSMA *et al.* (1992) and showed departures from Griend to the southwest between 8 and 18 August.

Changes in the composition of plumage types of knots (grey in winter, rusty-red in the summer breeding season) might indicate the arrival and departure of the two subspecies of knots probably occurring near Griend in July-September. *Canutus*-knots on passage should still be in breeding plumage since they moult their contour feathers only after arrival on the west African wintering grounds (PIERSMA *et al.*, 1992 and NTIAMOA-BAIDU, 1993 for reports of the arrival of breeding-plumaged adults in Ghana in September-October). In contrast, *islandica*-knots should change from red to grey as they replace their breeding plumage by a winter plumage in the Wadden Sea (BOERE, 1976; DAVIDSON & WILSON, 1992). Therefore, flocks of knots encountered on the high-tide roosts or on the low-water feeding grounds were regularly checked for plumage composition. To do so, a sample of more than 100 individual birds was scanned by telescope and each assigned to one of three categories: (1) a completely grey winter plumage or a trace of the rusty-red breeding plumage, (2) 1/4 to 3/4 breeding plumage and (3) more than 3/4 breeding plumage. Surprisingly, juveniles were only rarely observed.

3.2. BIRD MOVEMENTS AND FEEDING DISTRIBUTION

Movements to and from Richel to the feeding areas around Griend were monitored as often as possible and the approximate flight trajectories pencilled on a map. When on the island, we went out on the intertidal flats during most low water periods. We recorded the approximate time in the field and noted the area checked for the presence of knot flocks on maps along with a description of observer movements. The positions and sizes of encountered knot flocks were also recorded on the map, often based on triangulation of compass bearings taken in the field (usually on the lighthouse in West-Terschelling, the beacon on Griend and the highest church tower in Harlingen). Finally, flight paths of recorded flocks and the timing of movements were recorded on maps of the area. The daily map recordings served as the basis for the description of area use and movements of knots over the study area. To avoid biases in the estimates of area use due to unequal area cover during observation trips, we only included observations of flocks

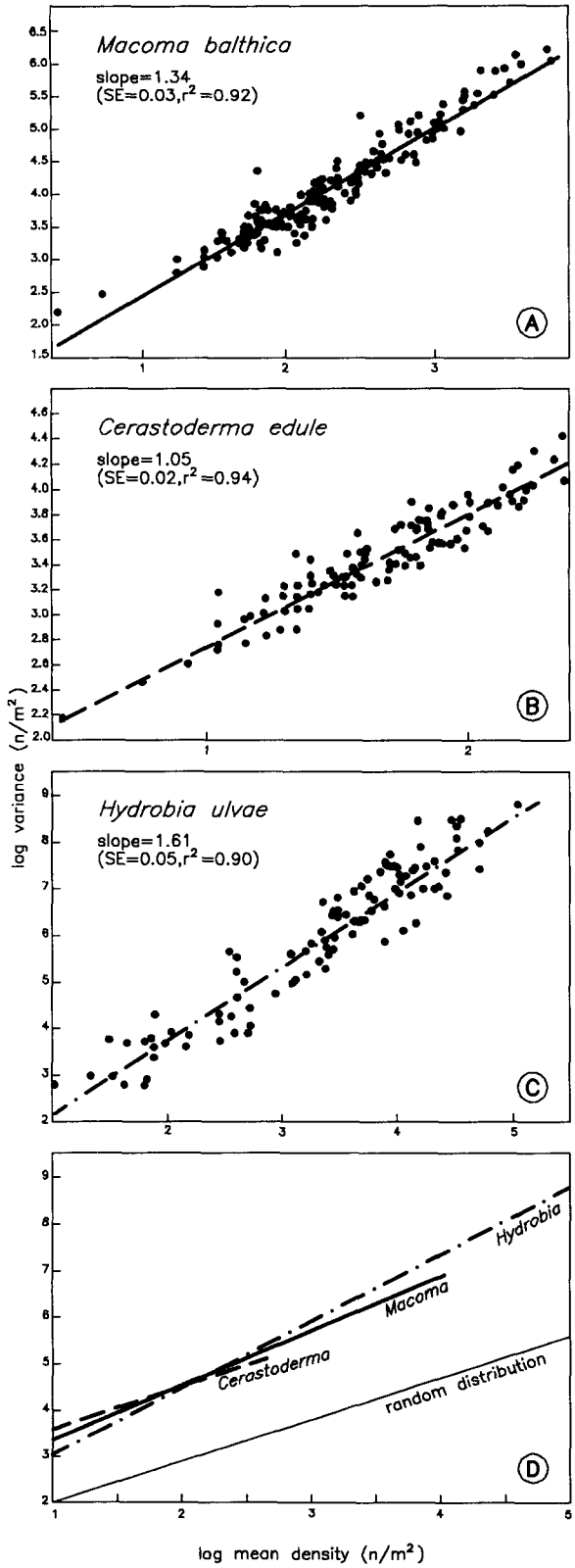


Fig. 3. The log of the variance as a function of the log of mean density (n/m^2) in (A) *Macoma balthica* (167 times 20 cores of 1/56 m^2), (B) *Cerastoderma edule* (152 times 20 cores of 1/56 m^2), and (C) *Hydrobia ulvae* (116 times 5 cores of 1/56 m^2). The estimated slopes from the resulting linear regressions are given in the figure. The intercepts are respectively 13.5 (or 13.5/56=0.24 per core), 50.1 (0.89) and 3.5 (0.06). Data from all sampling points and years taken together. In (D) the three species are compared with each other and with the predicted line of a random distribution of the molluscs with respect to a sampling area of 1/56 m^2 (*i.e.* where variance equals mean).

made in any one of the four sectors around the island (of fairly similar surface area) indicated in Fig. 2C, and for which we know that the timed visit per observation day was close to the average length (3-5 h). As *canutus*-knots visited Griend for a short period in relatively low numbers, we were unable to collect many relevant data on this subspecies. Records of feeding distribution are, therefore, from mid-August onwards and refer only to the *islandica*-subspecies.

3.3. FOOD ABUNDANCE

The total density of molluscs in the study area was determined by taking series of cores at fixed stations at intervals of 500 m on several transects starting 100 m offshore from the high-tide mark and pointing in different directions (Fig. 2C). If observations on the food and feeding of knots made it necessary, we sampled additional stations. All sampling stations are indicated in Fig. 2C. We were unable to sample the northern sector of the intertidal flats in 1989 in view of the extensive reworking of these sediments during commercial dredging of edible cockles *Cerastoderma edule* in September and October 1988. The layer of dead shells which normally occurs at a depth of 20-50 cm due to the activity of the polychaetes *Arenicola marina* and *Heteromastus filiformis* (CADÉE, 1976, 1979) was then completely mixed with the finer overlying sediment, making sieving impossible. However, it is likely that mollusc-densities were rather low there, and no knots occurred in this segment in 1989.

To sample balthic tellins, *Macoma balthica*, and edible cockles, *Cerastoderma edule*, we took 20 sediment cores of 1/56 m^2 down to a depth of 20 cm at each sampling station and sieved each of them over a 1-mm mesh. Mudsnails, *Hydrobia ulvae*, were sampled by taking 5 cores of 1/56 m^2 down to a depth of 3 cm and sieving over a 0.5-mm mesh. The content of each core was put into a separate identifiable plastic bag and stored frozen until laboratory treatment.

Later in the laboratory, the molluscs in each bag were counted and measured to the nearest mm (*Macoma*, *Cerastoderma*) or nearest 0.5 mm (*Hydrobia*). The maximum length of the bivalves was measured on mm-paper or with vernier callipers. The maximal lengths of *Hydrobia*-shells were measured under a binocular microscope with a micrometer

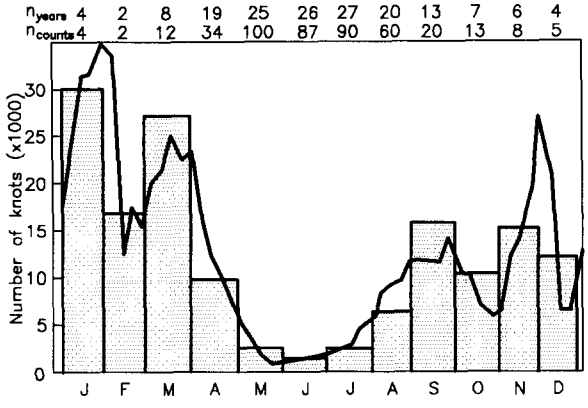


Fig. 4. Average seasonal changes in the maximum numbers of knots counted on or near Griend (usually during high tide) during the 29-year period 1964-1992. The histograms give the unweighted monthly averages, the curve shows the 5-week running average. The number of years from which counts are available and the total number of counts on which the monthly averages are based are given on the figure. For data sources, see Methods.

mounted in the eyepiece. In the bivalves, the soft parts were then separated from the shell (easy after freezing) and shells and meat of different-sized bivalves from one station were put in crucibles and dried in a ventilated drying oven at 55-60°C to constant mass. For *Hydrobia*, entire animals were dried per length class. The dry masses of the crucibles containing the entire snail, the bivalve-meat, or the bivalve-shells were then weighed and incinerated at 550°C for two h. After cooling in a desicator, the crucibles plus content were reweighed and finally the empty masses of the crucibles were obtained. In this way we determined the dry mass (DM), ash mass and ash-free dry mass (AFDM) of the meat (DM_{meat}, $AFDM_{meat}$) and shell (DM_{shell}, $AFDM_{shell}$) fraction in bivalves, and of the entire animal in *Hydrobia* (DM_{total}, $AFDM_{total}$).

The depth of *Macoma* was determined by cutting up cores of 1/56 m^2 in thin vertical slices until one was encountered. The distance between the upper edge of the shell and the surface was then measured (see fig. 1 of ZWARTS, 1986, for an illustration). We checked whether any sediment was lost from the surface of the core by plugging in a 'surface indicator' before taking it. In case of sediment loss, we corrected the measured depths accordingly. Individual *Macoma* were assigned to depth categories of 0.5 cm above a depth of 5 cm, and of 1 cm below 5 cm depth. In the laboratory, $AFDM_{meat}$'s of the individual *Macoma* were measured.

The accuracy with which mollusc densities are described by our sampling regime depends on the spatial pattern of the molluscs, and both can be summarized in plots of variance on mean density (*e.g.* BEUKEMA *et al.*, 1983), and most conveniently as log-log plots (TAYLOR, 1961; VÉZINA, 1988; MEIRE *et al.*, 1989 and references therein). Unity slope (variance equals mean) indicates a random distribution and higher variance values indicate increasing levels of aggregation. Fig. 3 shows that all three mollusc species exhibited a more or less aggregated pattern of distribution. The presented slopes are similar and of the same magnitude as those listed by VÉZINA (1988) and by MEIRE *et al.* (1989) for other macrobenthic species.

3.4. DIET OF KNOTS

The diet of knots was described by the analyses of droppings according to the methods outlined in detail by DEKINGA & PIERSMA (1993). Briefly, counted numbers of droppings were collected on the intertidal feeding areas at regular intervals. We collected them either with a spoon or with a (shell-) valve. Droppings were stored frozen, then dried at 55-60°C to constant mass, and sieved over a 300-µm mesh. The shell mass retained on this sieve was used to estimate the total shell mass in the faeces (equations in DEKINGA & PIERSMA, 1993). Sieved shell fragments were sorted to species and the species' contributions weighed. The total length of partially broken *Hydrobia* shells, and the height of intact hinges of *Macoma* and *Cerastoderma*, were measured under a binocular microscope with an ocular micrometer. Observer-specific regressions of hinge height on shell length were fitted to estimate the size distribution of ingested molluscs (see DEKINGA & PIERSMA, 1993). The compositional analyses of shell and meat in terms of ash, dry mass and AFDM, described above, yielded the site- and time-specific ratios to translate the species-specific shell masses into the contributions in biomass terms of the various mollusc species to the diet of knots (details in the Appendix).

4. RESULTS

4.1. SEASONAL OCCURRENCE OF KNOTS

The occurrence of knots on Griend was strongly seasonal (Fig. 4). On average, they numbered a few thousand in May-July, 10-15000 in September-December and 15-30000 in January-March. The 5-week running average shows, more clearly than the monthly averages, that numbers of knot peaked twice, both in autumn (a first peak in September, a second in late November) and perhaps in early spring (a first peak in January, a second in late March, but note the low number of February-counts). On three occasions at least 100000 knots were counted on Griend: in the 3rd week of March 1984, the 3rd week of September 1986 and again in the 3rd week of October 1986. The autumn peaks may represent an actively moulting (September) and post-moulting

wave (November) of knots, which were both on their way to the British estuaries (see *e.g.* DAVIDSON & WILSON, 1992; POOT & ROELEN, 1993). SHEPHERD (1992) shows that the strongest westward movement of knots into the Wash occurs in the last decade of November, *i.e.* at the same time as the second autumn-peak on Griend. The early spring peaks may represent return movements to the Wadden Sea in the course of winter and spring (DAVIDSON & WILSON, 1992).

A more detailed picture of the occurrence of knots during the study periods in 1988-1992 is given in Fig. 5. Even when counts were carried out daily, the maximum numbers observed on successive days fluctuated strongly. The temporary decrease in numbers in late September 1988 coincided with a period of heavy northwesterly storms when the flats around Griend hardly became exposed. Knots apparently remained on or near Richel, then their high-tide roost. As soon as the weather cleared up and when the intertidal flats became available again, the knots returned to Griend in similar numbers as before the stormy period (*ca* 20000 birds). The remaining fluctuations shown in Fig. 5 may genuinely represent the passage of successive waves of knots. In 1989 there were two peaks in early September and early October, in 1990 in mid-August and late August, and in 1991 in early August and in September. Departures to the southwest, of what are likely to be *canutus*-knots, were observed between 8 and 18 August in all years (see also PIERSMA *et al.*, 1992). This is indeed the time that the numbers decreased sharply in 1991. Especially for 1991, the steep decline in the proportion of birds in breeding plumage (Fig. 6) and, correspondingly, the increase of birds in an intermediate plumage, support the interpretation that the birds present in late July and early August are *canutus*-knots on their way to West Africa. Only there, they moult into a full winter plumage. The arrival, from 10 August onwards, of moulting *islandica* birds with incomplete breeding plumages is also reflected in Fig. 6. The rather high percentage of birds in winter plumage in late July/early August, may reflect the presence of oversummering immature knots (presumably *islandica*), which were later swamped by the arriving adults.

In late July and early August, knots always roosted on or near Griend; they even roosted in areas of open saltmarsh vegetation in the centre of Griend, a phenomenon which is well documented by Van De Kam's photographs in VEEN & VAN DE KAM (1988). From 15 August onwards (when *islandica* was the predominant subspecies), roost-site choice between Griend and Richel was dependent on the height of high water

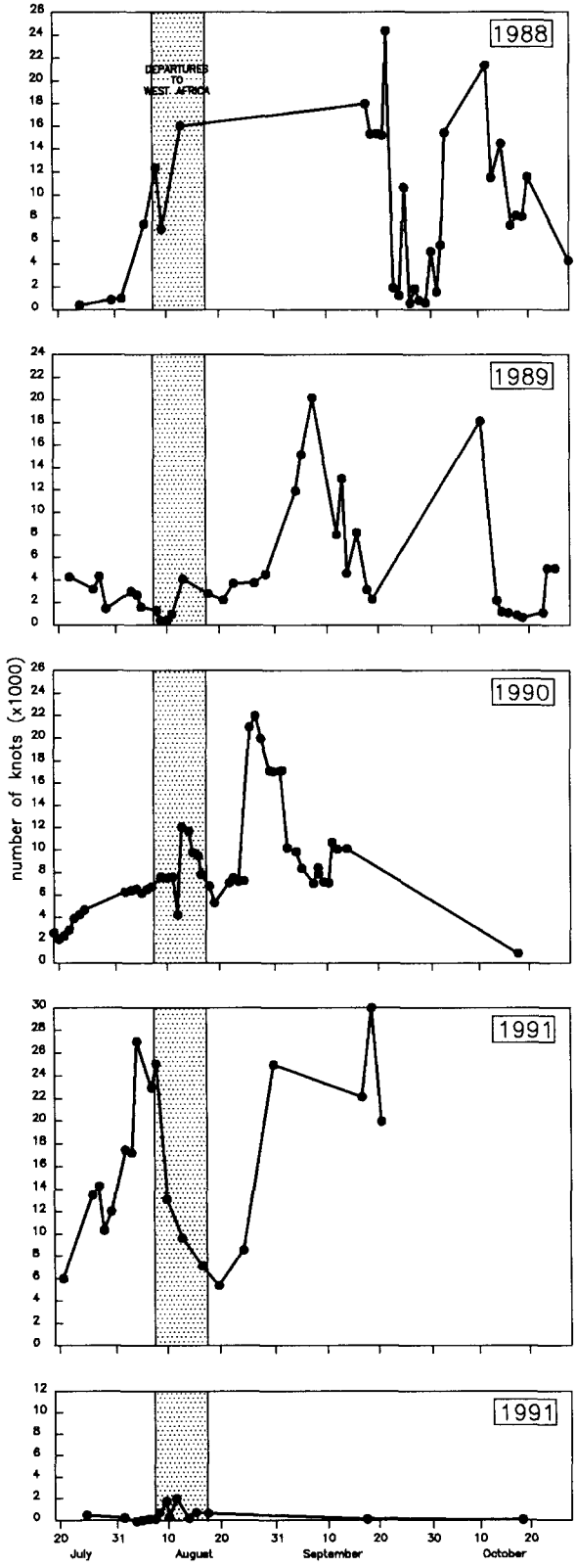


Fig. 5. Changes in the numbers of knots occurring on the flats around Griend in July-October periods in the five intensive-study years 1988-1992. This figure gives a sum of the numbers roosting on Griend and those flying onto Richel during the higher high tides (see Fig. 7).

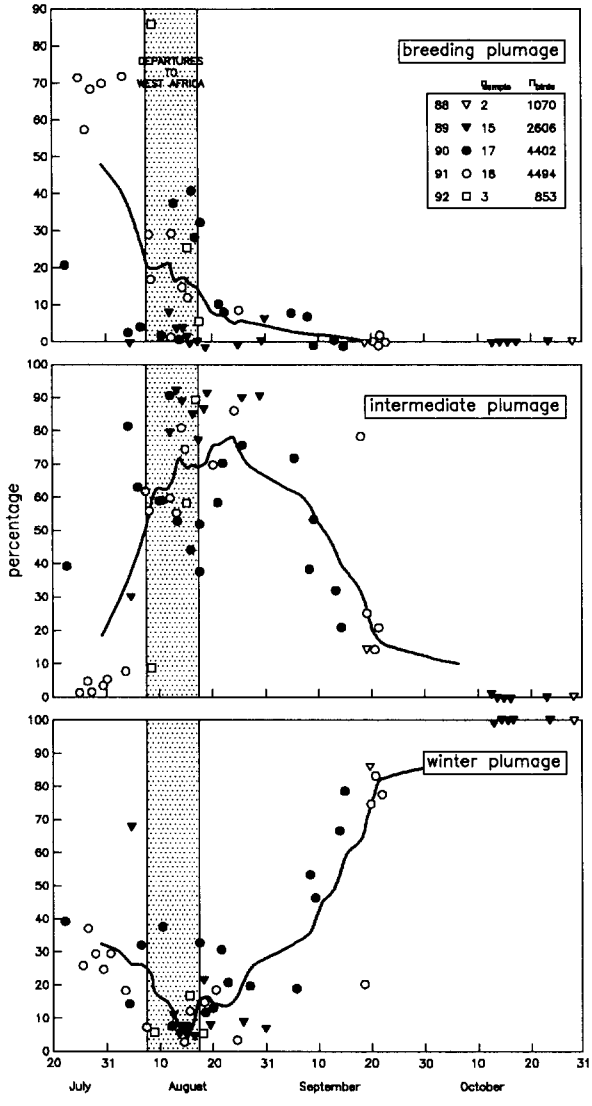


Fig. 6. Seasonal changes in the plumage composition of knots occurring on or near Griend in July-October 1988-1992. The period during which departures to West Africa were observed is indicated by the shaded bar (based on data presented by PIERSMA *et al.*, 1992: fig. 5). The line gives the running average over five successive data points.

(Fig. 7). At water levels higher than 70 cm above mean tide level, the majority of knots roosted on Richel, at lower high-water levels most knots roosted on Griend, but never in the well-vegetated centre of the island.

Numbers of knots occurring on Griend in August-October were of about the same magnitude in the years 1988 to 1991 inclusive (Fig. 5). Large numbers of (*canutus*) knots occurred in early August 1991, but very few knots were seen in 1992. To evaluate whether the numbers of knots that we observed between 1988 and 1992 were much different from those counted earlier, average knot numbers in two periods (22 July-11 August: *canutus*; 18 August-20 October: *islandica*) were plotted against year (1964-1992), based on all counts made between 1964 and 1992 (Fig. 8). Although the data are rather fragmentary for the second annual period, it is clear that there are no apparent long-term trends in the numbers of knots. What we can safely state, though, is that numbers of knots occurring between 22 July and 11 August were exceptionally high in 1991 (first time in 24 years, a probability of 4.2%) and that in 1992 numbers of knots occurring in July and August were exceptionally low (probabilities of respectively 4.0% and 7.1%). The small probabilities, at about the 5-% significance level, suggest that the high and low numbers in 1991 and 1992 were no simple stochastic events.

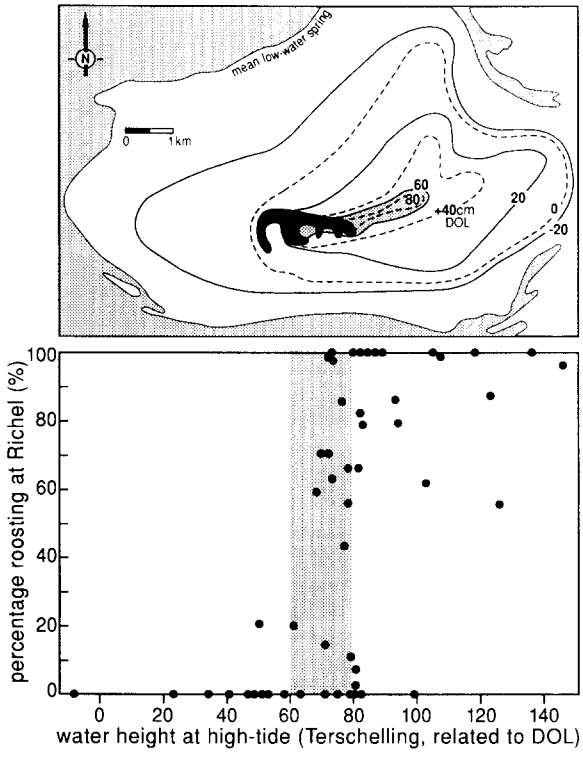


Fig. 7. Relative use of Griend by knots during high water in relation to the high-water level at West-Terschelling from 15 August to 31 October 1988-1991 (lower panel). The map (top panel) indicates the extent to which the sandflats are exposed at different water levels relative to Dutch Ordinance Level.

4.2. AERIAL PREDATORS

We observed individuals of eight species of aerial predators (6 raptors, 1 owl and 1 gull; Table 1) that could potentially kill knots and other shorebird species (BIJLSMA, 1990; pers. obs.; various pers. comm. to TP). Table 1 is not complete, since the presence of raptors on the island could go unnoticed for days. Panics among the waders on Griend did not automatically imply the presence of raptors, as waders also strongly reacted to overflying great black-backed gulls *Larus marinus*. Merlins, peregrines and short-eared owls were observed to hunt roosting shorebirds. These attacks normally resulted in a massive panic among the waders. Upon detection of a raptor they took flight and performed complicated evasive movements in dense flocks. The two raptor species most dangerous for knots are peregrine and, to a lesser extent, merlin. Both species regularly migrate through the area and overwinter in the Wadden Sea. Peregrines are known to take up residence on the wardens' house in some winters (VEEN & VAN DE KAM, 1988; P. Wolf, pers. obs.). We did not find the remains of knots as raptor-prey during the study period, but found pluckings of knots in February and April 1990 when a female peregrine was present on the island.

The centre of Griend was also used as a roost by herring gulls *Larus argentatus* and great black-backed gulls. The latter species, the largest European gull, was the only predator that was actually observed eating knots. On two occasions an adult great black-backed gull flew in from the sandflats with a dead knot in its bill. The knots were washed (or wetted) in a small tidal pool in the saltmarsh and swallowed whole. Although a flying knot has little to fear from such gulls, a roosting bird could be picked up by a low-flying gull coming into the roost. Great black-backed gulls are also present on Richel for most of the year (ZEGERS & KWINT, 1992), but here a knot's view would not be obstructed by vegetation.

4.3. DIET OF KNOTS

Two bivalves, *Macoma* and *Cerastoderma*, and one gastropod, *Hydrobia*, made up the bulk of the diet of knots feeding on the intertidal flats around Griend. In August, knots were sometimes observed to hunt for the occasional shrimp *Crangon crangon*, shorecrab *Carcinus maenas* and ragworm *Nereis diversicolor*, but such observations were few and far between. Knots were pretty clumsy in capturing and handling such actively moving prey. On a few occasions knots fed on mussels *Mytilus edulis*.

The contribution of the four mollusc species to the diet of knots in the five study seasons according to the dropping analyses is presented in Fig. 9. The diet for each month is given, but August is split into two periods. Early August denotes the early period when

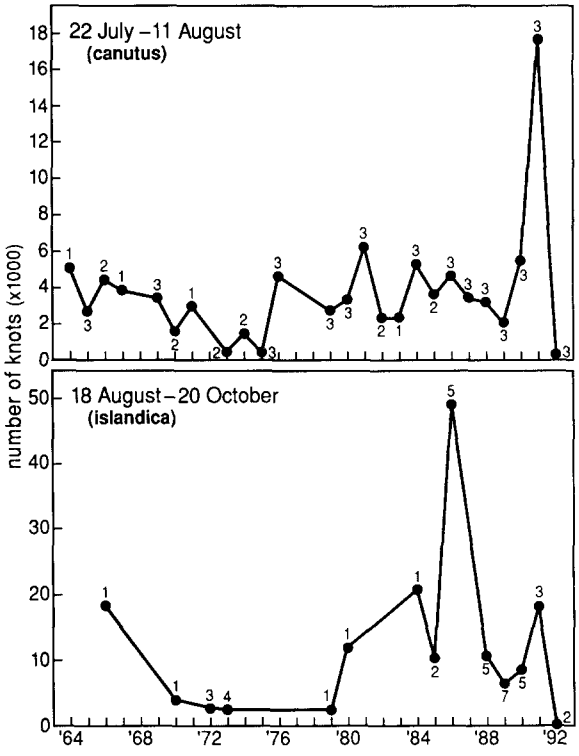


Fig. 8. Trends in the numbers of presumed *canutus*-knots (A) and *islandica*-knots (B) counted on or near Griend in 1964-1992. Averages of all available counts are plotted against year; the number of counts is indicated. Note that the y-scales of (A) and (B) are rather different.

most knots around were probably *canutus*, and late August is the latter half of August when *islandica*-knots were around in big numbers. *Macoma* contributed most to the ingested biomass in August in 1988 and 1989. In 1988, 1989 and 1991 the contribution of *Macoma* to the diet decreased in the course of autumn. In 1988 and 1989, *Macoma* was replaced by *Hydrobia*, but in August-September 1990-1992 *Cerastoderma* was an important alternative prey. Only in mid-August 1992, did *Mytilus* contribute more than 10% to the diet. This was caused by the inclusion of droppings from a flock of 250 knots feeding on a small patch of mussel spat south of Griend.

To define the part of the food stock suitably sized for ingestion by gape-limited knots, the lengths of *Macoma*, *Cerastoderma* and *Hydrobia* fed upon in September in the different years are presented in Figs 10, 11 and 12, respectively. The ingested lengths of *Macoma* varied between 3 and 18 mm. *Cerastoderma* between 3 and 17 mm long were estimated to be taken. Shell-lengths greater than 14 mm were rare, however, even though some captive knots are also able to ingest such large sizes (T. Piersma & J.

TABLE 1

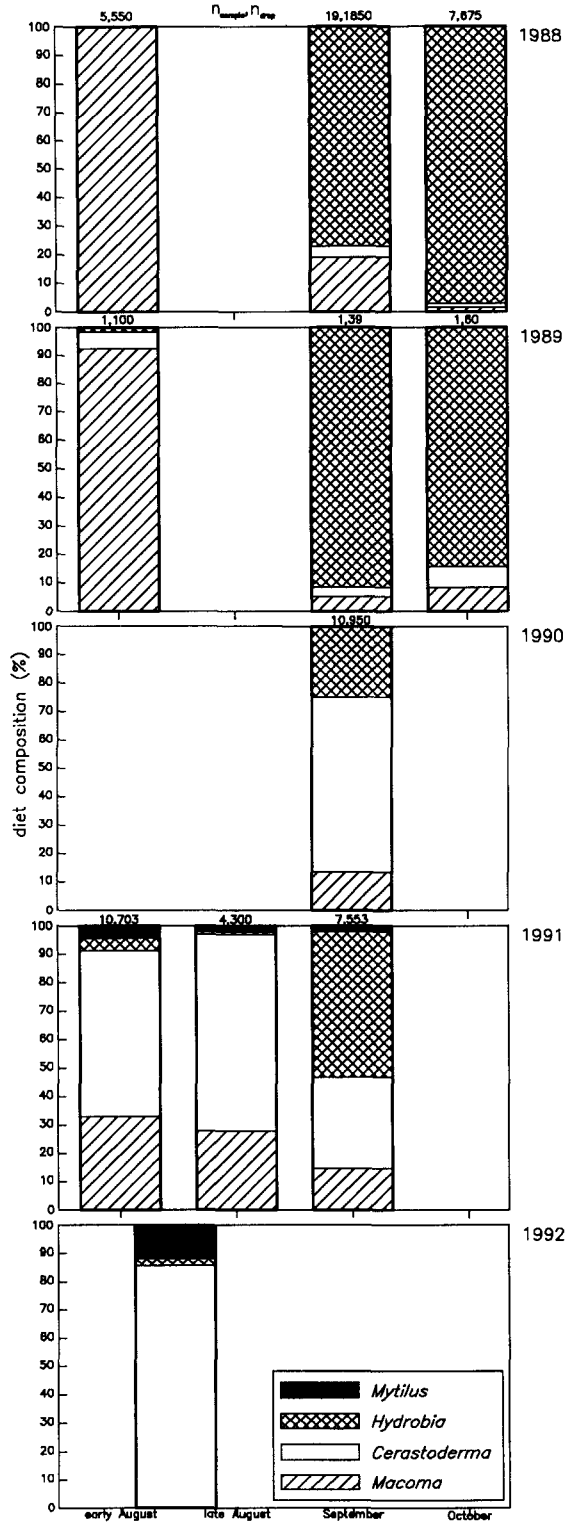
Occurrence per decade of aerial predators on Griend in the late July-October periods of 1988-1992. Data are based on daily observations of variable intensity and on intensive weekly counts covering the whole island. Each X denotes a positive observation of at least one individual bird of prey in the particular decade. If a year is not listed, no individuals of the particular species were observed.

		July	*August*			*September*			*October*		
		3	*1*	*2*	*3*	*1*	*2*	*3*	*1*	*2*	*3*
Marsh Harrier	1989		X	X	X		X				
Circus aeruginosus	1990			X			X				
	1991					X	X				
Hen Harrier	1988										X
Circus cyaneus	1989			X			X			X	
	1990		X								
	1991		X				X				
Sparrowhawk	1988						X	X		X	
Accipiter nisus	1989						X			X	
	1990						X				
Kestrel	1989			X	X	X	X			X	X
Falco tinnunculus	1990					X	X				
	1991			X	X						
Merlin	1988						X	X		X	X
Falco columbarius	1989									X	
	1990				X						
	1991						X	X			
Peregrine	1988								X	X	X
Falco peregrinus	1989				X	X	X			X	X
	1990		X								X
	1991						X	X			
Short-eared Owl	1990			X	X						X
Asio flammeus	1991					X	X				
	1992	X	X	X	X						
Great black-backed gull	1988	X	X	X	X	X	X	X	X	X	X
Larus marinus	1989	X	X	X	X	X	X	X	X	X	X
	1990	X	X	X	X	X	X	X	X	X	X
	1991	X	X	X	X	X	X	X	X	X	X
	1992	X	X	X	X	X	X	X	X	X	X

van Gils, unpubl. obs.). *Hydrobia* varied in length from 0.5 to 6.5 mm (Fig. 12). The differences in ingested size between the periods were pronounced. These differences might be related to variations in the relative availability of differently sized molluscs, and perhaps, to different selection criteria on part of the knots. Direct comparisons between the abundance of the molluscs on offer and the diet composition reconstructed from droppings collected simultaneously in this and other areas are in progress, but beyond the scope of this paper. There were no clearcut differences in the relative lengths of mollusc prey taken in early August (by *canutus*-knots) and in late August (by *islandica*-knots), indicating an apparent lack of subspecific differences in diet selectivity.

4.4. FOOD STOCKS

The distribution and abundance of the benthic food stocks can be expressed in various ways. We have chosen to present total densities and the densities of the size classes suitable for ingestion by knots (not too small, nor too large; see ZWARTS *et al.*, 1992 and Figs 10 and 11), together with the equivalent biomass



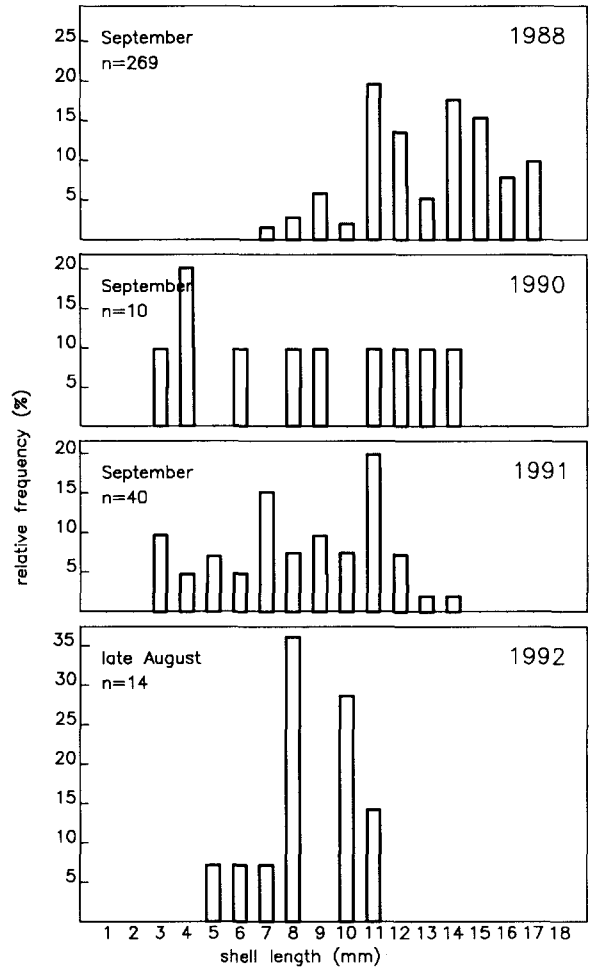
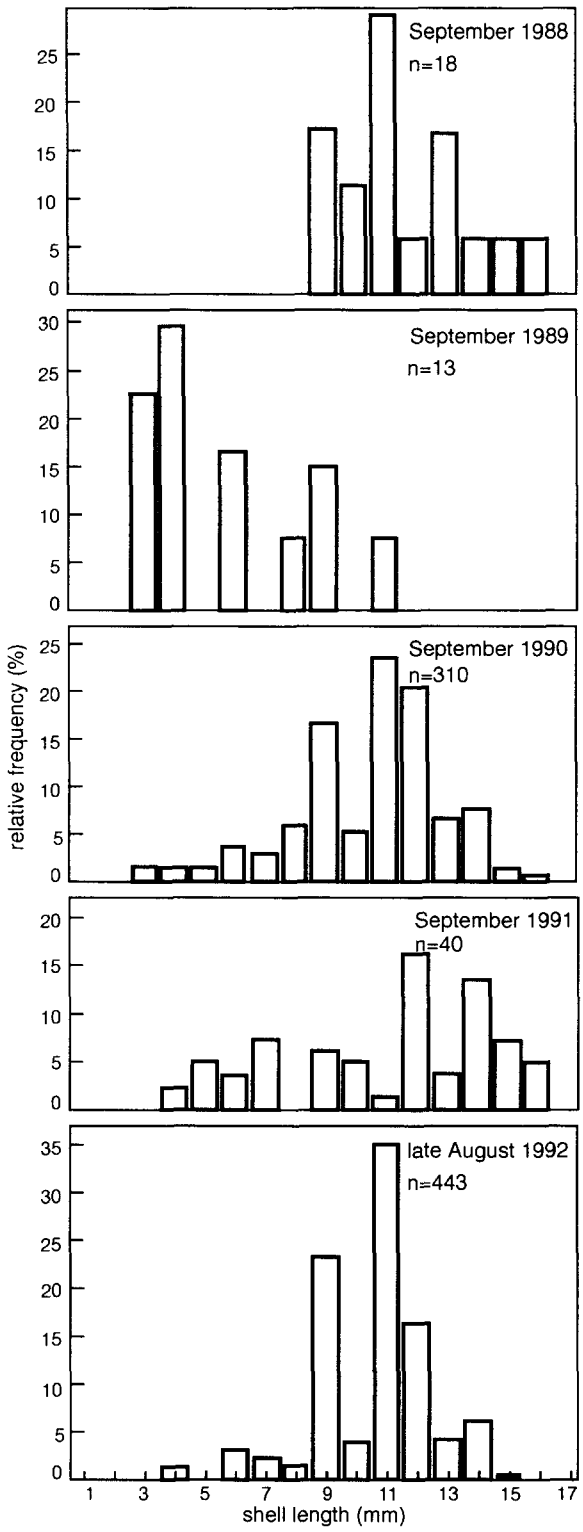


Fig. 10. Size-frequency distributions of *Macoma balthica* fed upon by knots on the intertidal areas around Griend in late August-September 1988-1992 based on the analysis of droppings.

figures, in the first place in tables (Tables 2-4). To illustrate the distribution patterns and changes over the years we also plotted the biomass values (both total biomass, and the biomass of suitably sized prey) per sampling station on a map (Fig. 13). To translate the frequency distributions of shell length (SL, mm) of the two bivalve species into biomass values ($AFDM_{meat}$, mg) per sampling station the following allometric equations were used. For *Macoma* AFDM-

Fig. 9. Diet composition in terms of biomass ($AFDM_{meat}$ in the bivalves and $AFDM_{total}$ in *Hydrobia*) of knots feeding on the intertidal areas around Griend in different times of the year in the period 1988-1992, based on the analysis of droppings. For each period the number of dropping samples (n_{sample}) and the total number of droppings included (n_{drop}) are indicated in the figure.



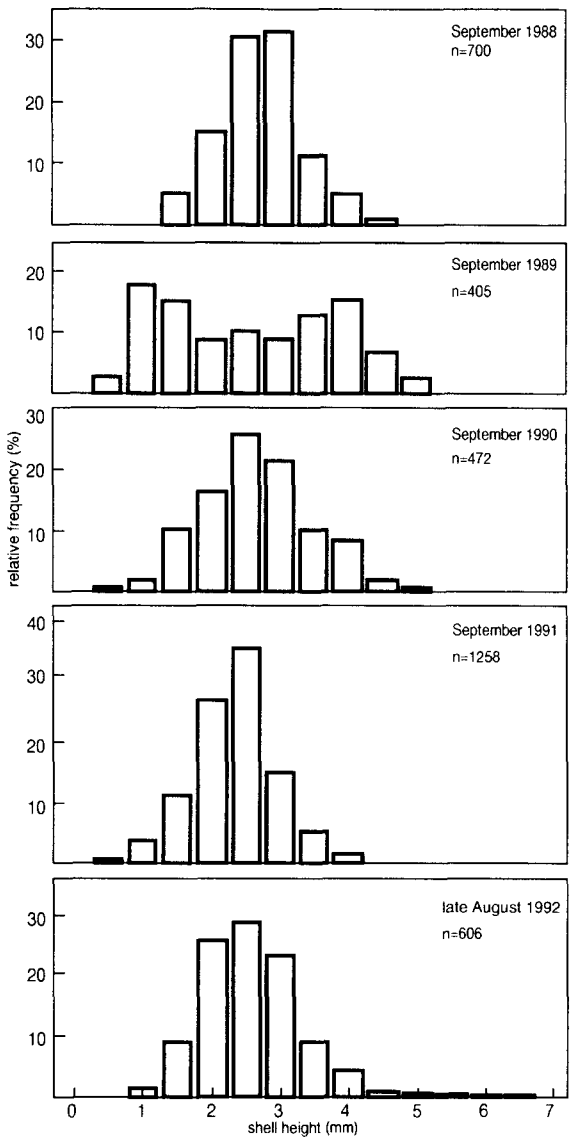


Fig. 12. Size-frequency distributions of *Hydrobia ulvae* fed upon by knots on the intertidal areas around Griend in late August-September 1988-1992 based on the analysis of droppings.

$_{meat}=0.0220 \cdot SL^{2.658}$ (n=1777, $r^2=0.95$, $p<0.00001$), for *Cerastoderma* $AFDM_{meat}=0.0246 \cdot SL^{2.723}$ (n=780, $r^2=0.94$, $p<0.00001$). An analysis of covariance, with shell length as the covariate, showed that within the

Fig. 11. Size-frequency distributions of *Cerastoderma edule* fed upon by knots on the intertidal areas around Griend in late August-September 1988-1992 based on the analysis of droppings.

3-month period August-October there were no significant effects of year, sector and month on the slope of the log-log regression line of $AFDM_{meat}$ on shell length (for *Macoma*, year: F=10.07, p>0.1, sector: F=13.26, p>0.1, month: F=10.60, p>0.1; for *Cerastoderma*, year: F=2.33, p>0.1, sector: F=7.31, p>0.1, month: F=3.86, p>0.1), but see ZWARTS (1991) and ZWARTS & WANINK (1993) for examples of clear seasonal patterns. For *Hydrobia* we always measured the biomass ($AFDM_{total}$) directly for the whole batch per sampling station, and such an analysis can therefore not be carried out. We did not correct for possible depth-effects on size-related biomass in the bivalves (*cf.* ZWARTS & WANINK, 1991), but we showed it to be unimportant in other sandy areas in the western Wadden Sea where knots occur in spring (T. Piersma, Y. Verkuil & I. Tulp, in prep.).

All the three prey species of knots show much spatial and between-year variation in their distribution and abundance (Fig. 13, and Table 2: *Macoma*, Table 3: *Cerastoderma*, and Table 4: *Hydrobia*). In the northern and eastern sectors, biomass of *Macoma* tended to increase with increasing distances from the island (correlating with lower lying sandflats) in all years (Fig. 13). Densities of spat were usually highest on the high flats close to the island, hence the sometimes high local biomass values in years of good spatfall, *i.e.* 1989, 1990 and especially 1991 (Fig. 14). In 1988, *Macoma* was abundant and included many >2nd year animals. In the northern sector these *Macoma* largely disappeared as a side-effect of the intense cockle-dredging in 1988, and they never recovered. Remarkably, very little of the large spatfall in 1991, especially in north and east, survived to August 1992, perhaps an indirect effect of the changes in sediment characteristics described above (and see PIERSMA *et al.*, 1993a).

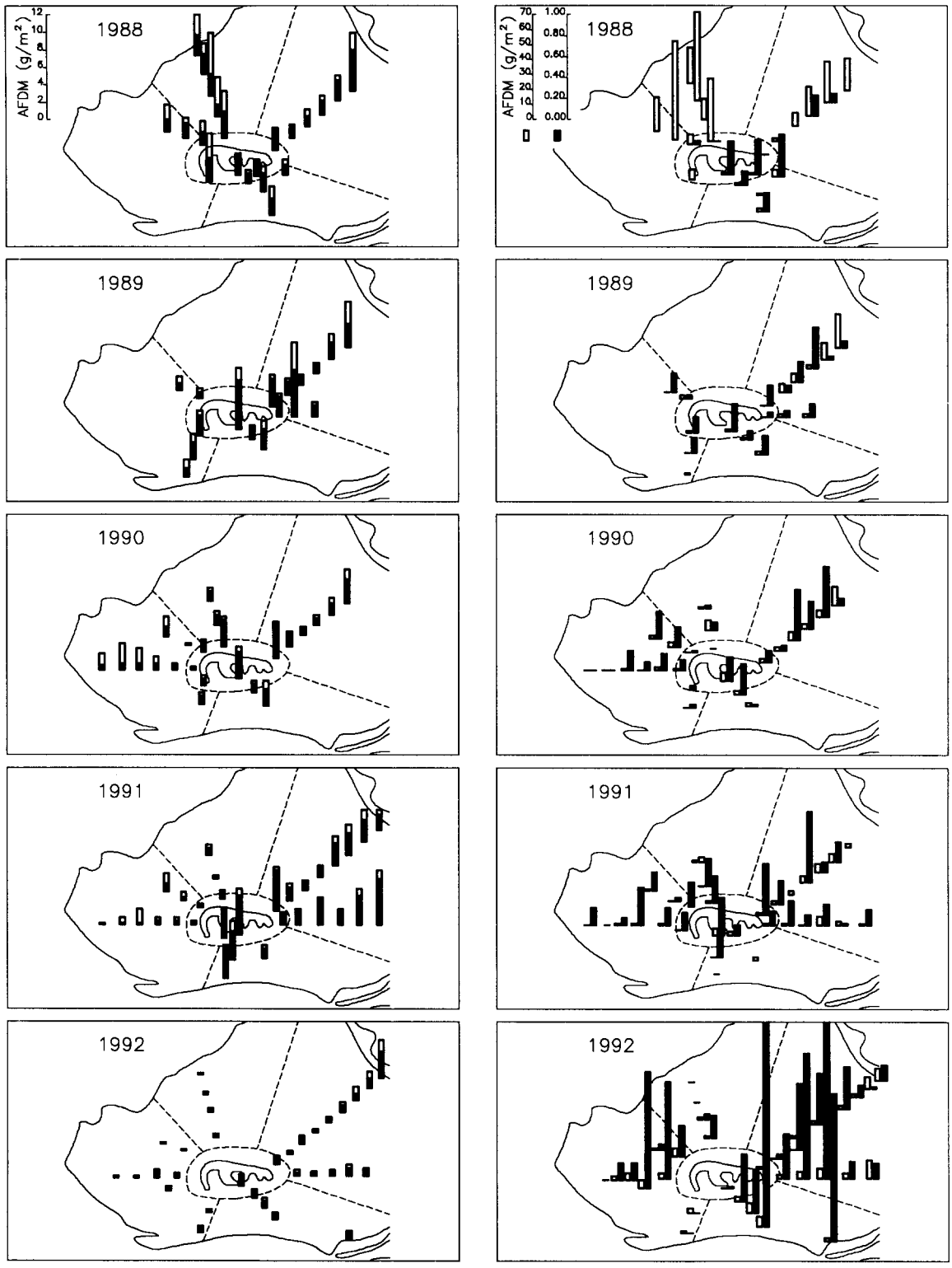
The high densities of large-sized *Cerastoderma* (Figs 13 and 15) found in the northern and eastern sectors in 1988 were removed by the shell fisheries in the same year, and the cockle population never recovered. On the high flats close to the island some spatfall occurred in all years, but only in August 1992 was there heavy spatfall with densities of over 100 per m^2 at some sampling stations. Even in that year hardly any *Cerastoderma* settled in the overfished

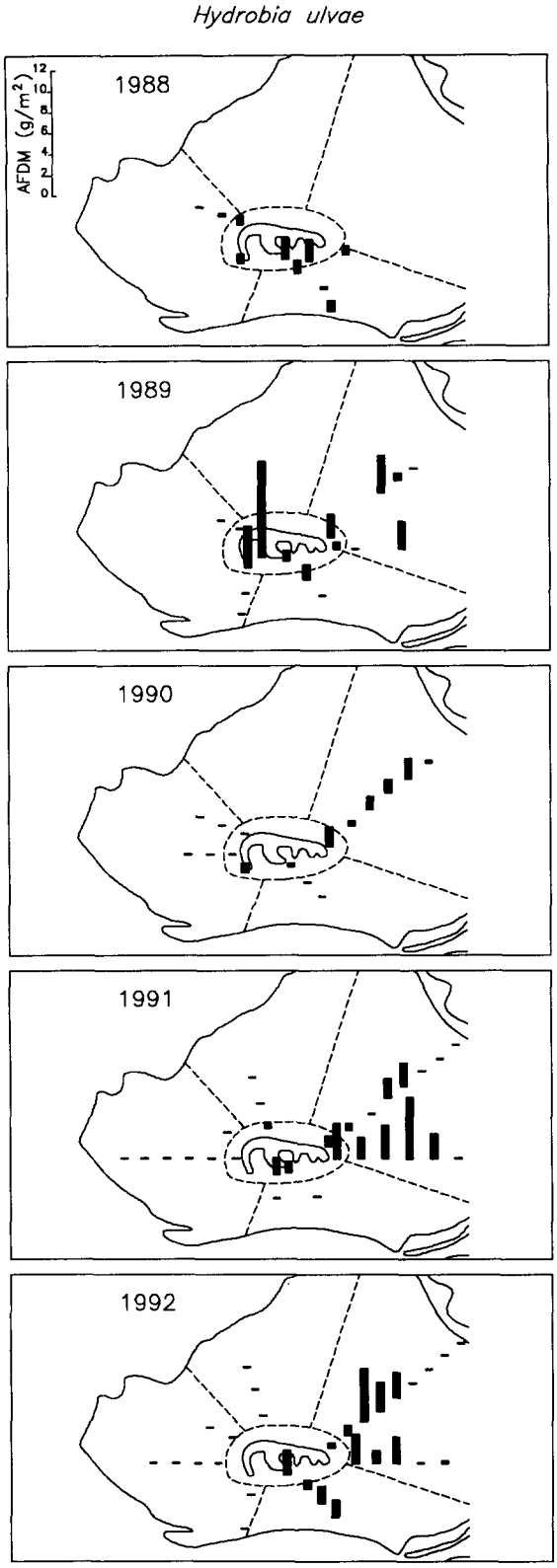
TABLE 2

Summary statistics of the abundance of *Macoma balthica* around Griend in August-September periods of 1988-1992. For delimitation of the different sectors around Griend, see Fig. 2C. The abundance values for 'all flats' do not include the results of the nearshore samples ('island'), since knots rarely occurred there. Suitable sizes are 3 to 18-mm long *Macoma*.

Variable	*Area*	*1988*			*1989*			*1990*			*1991*			*1992*		
		mean	*SD*	*(n)*	*mean*	*SD*	*(n)*	*mean*	*SD*	*(n)*	*mean*	*SD*	*(n)*	*mean*	*SD*	*(n)*
Density (n/m^2)	Island	750	756	(8)	1400	839	(9)	291	357	(6)	1846	2074	(8)	187	177	(2)
	West	87	25	(3)	230	188	(4)	59	25	(8)	25	18	(7)	30	18	(4)
	North	125	26	(6)	-	-	(0)	49	2	(2)	66	38	(2)	30	18	(4)
	East	395	262	(5)	650	504	(8)	179	274	(8)	600	637	(20)	175	103	(13)
	South	162	55	(5)	254	267	(6)	114	55	(2)	565	739	(3)	94	36	(4)
	All flats	200	177	(19)	423	418	(18)	111	178	(20)	438	592	(32)	104	95	(30)
Density suitable sizes (n/m^2)	Island	586	528		1361	713		287	355		1779	2012		184	178	
	West	74	21		213	185		46	28		18	15		34	19	
	North	87	23		-	-		42	10		63	41		29	19	
	East	307	145		605	476		174	276		573	585		167	103	
	South	151	56		226	224		106	63		557	729		90	38	
	All flats	160	121		392	391		103	180		418	553		99	93	
Biomass ($gAFDM/m^2$)	Island	4.98	2.54		4.68	2.47		2.93	2.03		3.41	2.73		1.40	0.45	
	West	3.37	0.63		2.74	0.38		2.37	0.96		1.24	0.84		0.55	0.28	
	North	6.58	1.98		-	-		2.19	0.08		1.04	0.81		0.37	0.14	
	East	3.68	2.31		4.05	3.37		2.02	1.22		3.44	1.98		1.45	1.46	
	South	3.17	1.44		3.31	1.36		2.63	1.44		4.07	1.80		1.01	0.20	
	All flats	4.41	2.26		3.51	2.35		2.24	1.02		2.87	1.98		0.98	1.06	
Biomass suitable sizes ($gAFDM/m^2$)	Island	3.34	1.43		3.78	2.07		2.57	1.84		3.02	2.40		1.22	0.38	
	West	2.03	0.47		1.57	0.53		1.12	0.26		0.46	0.28		0.52	0.24	
	North	2.61	0.93		-	-		1.54	0.21		0.74	0.39		0.34	0.20	
	East	2.81	1.74		2.63	1.89		1.54	0.93		2.74	1.47		1.03	0.90	
	South	2.03	0.62		2.46	0.76		1.80	0.77		3.37	1.78		0.84	0.19	
	All flats	2.42	1.07		2.34	1.37		1.40	0.66		2.18	1.64		0.76	0.66	

Macoma balthica *Cerastoderma edule*





northern sector, perhaps also due to a change to a sandier sediment (PIERSMA *et al.*, 1993a).

Regrettably, *Hydrobia* was not sampled in all sectors in 1988 and 1989 (Table 4), but looking at the distribution maps only small changes from year to year are apparent (Fig. 13). *Hydrobia* always occurred in highest densities on the high flats just east and southeast of the island. The low-lying western and northern sectors, most exposed to wind and wave action, were not inhabited by *Hydrobia*. Size-frequency distributions were more similar between years in *Hydrobia* (Fig. 16), than in the two bivalves (Figs 14 and 15). Small, and presumably recently settled, *Hydrobia* were most common in 1989. Little recruitment was apparent in 1992.

Taking the knot point of view, even the biomass densities of suitable size classes do not represent the harvestable (*sensu* ZWARTS *et al.*, 1992) amounts of food, since the prey may bury beyond the reach of their 3.5-cm long bill. As *Cerastoderma* of the suitable size classes never bury deeper than 2 cm (fig. 3 of ZWARTS & WANINK, 1989), and since *Hydrobia* does not go deeper than 0.5 cm (fig. 3 of MOURITSEN & JENSEN, 1992), we measured only the depth distribution of *Macoma* at regular intervals at as many stations as possible. In all three years (1988, 1989, 1991) that a comparison between months can be made, suitably sized *Macoma* buried deeper from August onwards (Fig. 17), decreasing the fraction accessible to knots from 13-47% in August to 2-30% in September (a seasonal pattern also found elsewhere: READING & MCGRORTY, 1978; ZWARTS & WANINK, 1993). The fraction accessible in August varied a lot between years, from 47% in 1989 to only 13% in 1992, *i.e.* a factor 3.6. As the total biomass of *Macoma* varied between 4.41 g AFDM per m^2 in 1988 and 0.98 g AFDM per m^2 in 1992 (Table 2), *i.e.* a factor 4.5, the accessible fraction is as important a factor as total biomass in determining food abundance for knots.

A summary of the changes in the abundance of *Macoma*, by far the most important prey taken by knots when they were common (as in 1988) (Fig. 18), shows a continuous decrease in biomass of ingestible *Macoma* from 1988 to 1992 (Spearman rank-correlation coefficient, r_S=-0.95, $p<0.05$, one-tailed test), and a continuously decreasing harvestable biomass (r_S=-0.80, $0.05<p<0.1$). Around Griend, the major prey species of knots has become scarcer in the course of the study.

Fig. 13. Spatial and yearly variation in the overall abundance of balthic tellins *Macoma balthica*, edible cockles *Cerastoderma edule* and mudsnails *Hydrobia ulvae* near Griend in August-October in the period 1988-1992. For each sample location (for the bivalves 20 cores, for the mudsnail 5 cores, 1/56 m^2, 1-mm sieve), the (left) bar indicates the total biomass, and the hatched part of the (right) bar the biomass of bivalves of suitable length (*Macoma*: 3-18 mm; *Cerastoderma*: 3-14 mm).

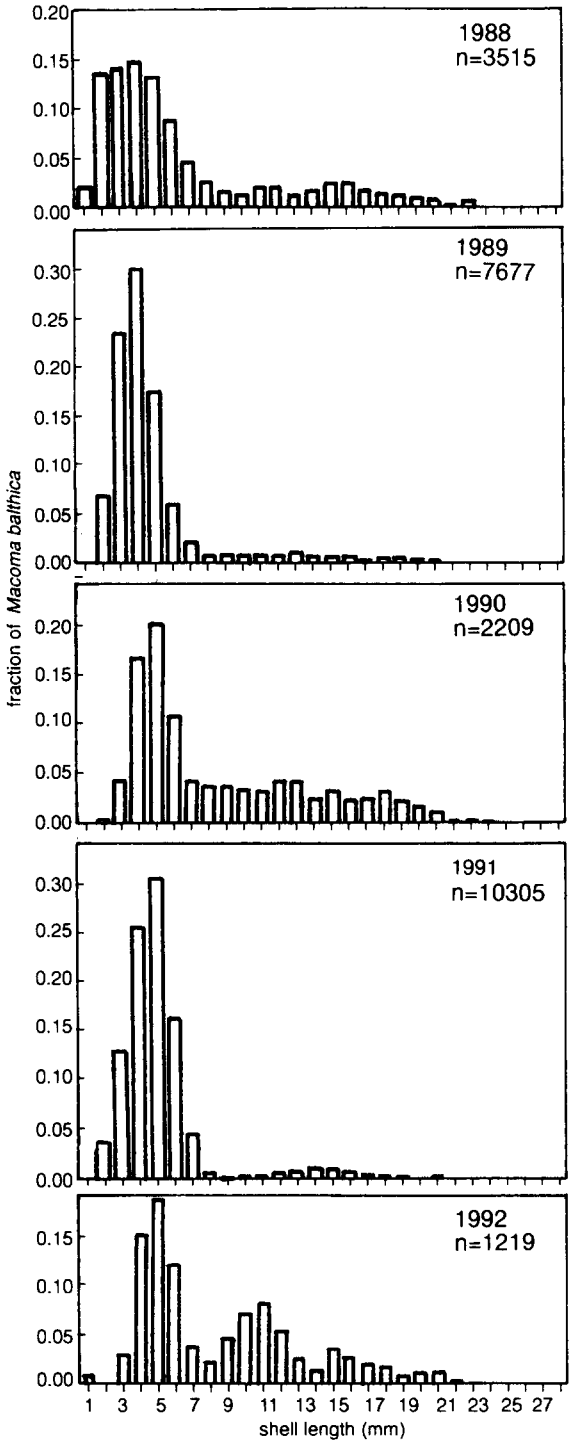


Fig. 14. Size-frequency distributions of *Macoma balthica* in August-September in the period 1988-1992. Based on the results of all overall density samples, including the near-shore ones. The total number of measured *Macoma* is indicated by the n-value.

Right. Fig. 15. Size-frequency distributions of *Cerastoderma edule* in August-September in the period 1988-1992. Based on the results of all overall density samples, including the near-shore ones. The total number of measured *Cerastoderma* is indicated by the n-value.

Far right. Fig. 16. Size-frequency distributions of *Hydrobia ulvae* in August-September in the period 1988-1992. Based on the results of all overall density samples, including the near-shore ones.The total number of measured *Hydrobia* (sometimes on a sampling basis) is indicated by the n-value.

4.5. FEEDING DISTRIBUTION

Since the observer effort (time spent per visit and area covered) was roughly similar in the four sectors around the island (see Methods), the probability of encountering flocks of knots can be compared between sectors (Fig. 19, top row). The likelihood of encountering knots was always highest in the eastern sector, always quite low in the southern sector (except for 1992, but see below), and variable for the western sector. Knots were regularly encountered north of Griend in 1988, but were rarely seen there in 1989 and 1990, after the cockle-dredging devastation of the northern flats in late September-early October 1988. Knots were only rarely observed feeding within 500 m from the island, even though high prey densities occurred there (Fig. 13). Only during storms were knots feeding in the lee of the island, either north of the dike (with southwesterlies) or southeast of the old island (at northwesterlies). Even then flock size never exceeded 500 birds.

The computation of the relative intensity of use of different sectors requires knowledge of the size of encountered knot flocks at low tide (defined as the period from 3 h before to 3 h after low tide). The frequency distribution of feeding flock sizes (Fig. 20) shows that, although most flocks are smaller than 1500 birds, the majority of knots occurring near Griend in 1988-1992 were nevertheless roaming about in flocks of 4000 to 15000 individuals. There were rather pronounced differences in the average size of the flocks in different sectors (Fig. 19, middle row). Knot flocks were largest in the east, and average flock size became smaller over the years in all sectors, except south. Over the period 1988-1991, this did not correlate with the knot numbers counted around high water near Griend or *en route* to Richel, which were rather constant (see Fig. 5). Flock sizes were very small everywhere in 1992, as were the numbers counted at high tide.

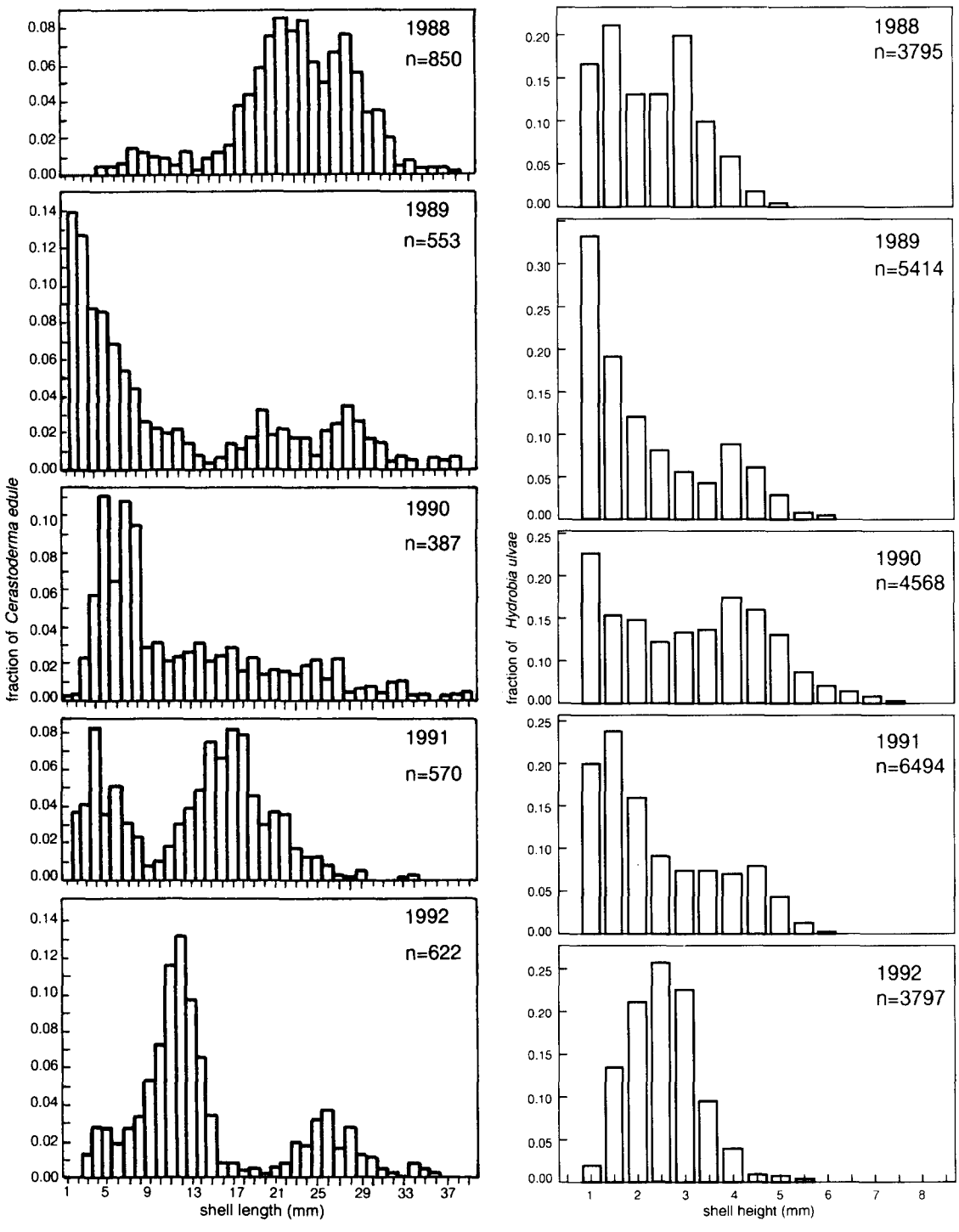

1988
n=850
1989
n=553
1990
n=387
1991
n=570
1992
n=622
fraction of Cerastoderma edule
shell length (mm)
1988
n=3795
1989
n=5414
1990
n=4568
1991
n=6494
1992
n=3797
fraction of Hydrobia ulvae
shell height (mm)

TABLE 3

Summary statistics of the abundance of *Cerastoderma edule* around Griend in August-September periods of 1988-1992. Suitable sizes for knots are 3 to 14-mm long *Cerastoderma*.

Variable	*Area*	*1988*	*1989*	*1990*	*1991*	*1992*
		mean SD (n)	*mean SD (n)*	*mean SD (n)*	*mean SD (n)*	*mean SD (n)*
Density	Island	61 60 (8)	69 68 (9)	20 27 (6)	50 51 (8)	16 15 (2)
(n/m^2)	West	122 61 (3)	12 5 (4)	14 11 (7)	18 13 (7)	48 47 (9)
	North	70 69 (6)	- - (0)	24 18 (2)	13 2 (2)	8 8 (4)
	East	142 92 (5)	72 25 (8)	58 41 (8)	48 35 (20)	63 43 (13)
	South	23 12 (5)	45 47 (6)	20 17 (3)	12 12 (3)	121 81 (4)
	All flats	85 77 (19)	50 39 (18)	33 34 (20)	36 32 (32)	59 55 (30)
Density	Island	15 25	51 62	13 20	32 41	7 6
suitable	West	0 0	6 4	11 9	11 10	30 38
sizes	North	0 0	- -	8 4	7 6	4 5
(n/m^2)	East	5 6	24 16	37 33	14 17	46 45
	South	11 7	30 31	12 12	7 11	84 69
	All flats	4 6	22 22	21 25	12 15	41 47
Biomass	Island	11.71 16.02	1.40 1.80	2.05 2.87	1.82 1.82	0.41 0.31
($gAFDM/m^2$)	West	53.76 23.12	1.04 0.94	2.10 1.99	0.69 0.48	4.18 2.95
	North	30.44 32.45	- -	5.05 4.07	0.92 0.86	1.20 1.08
	East	19.55 12.49	10.07 9.63	6.26 5.64	4.06 3.29	5.27 4.52
	South	3.06 2.12	2.72 3.20	2.33 1.37	0.88 0.58	6.92 2.91
	All flats	24.05 26.01	5.61 7.65	4.09 4.25	2.83 3.06	4.26 3.80
Biomass	Island	0.15 0.26	0.19 0.22	0.09 0.11	0.33 0.36	0.01 0.00
suitable	West	0.0 0.0	0.11 0.12	0.15 0.12	0.16 0.14	0.35 0.49
sizes	North	0.0 0.0	- -	0.07 0.05	0.19 0.18	0.08 0.11
($gAFDM/m^2$)	East	0.08 0.09	0.14 0.15	0.40 0.26	0.25 0.45	0.58 0.58
	South	0.20 0.14	0.18 0.10	0.13 0.18	0.08 0.14	1.36 1.06
	All flats	0.07 0.12	0.15 0.12	0.24 0.23	0.21 0.36	0.55 0.67

TABLE 4

Summary statistics of the abundance of *Hydrobia ulvae* around Griend in August-September periods of 1988-1992. Numbers are given in 1000's per m^2.

Variable	*Area*	*1988*	*1989*	*1990*	*1991*	*1992*
		mean SD (n)	*mean SD (n)*	*mean SD (n)*	*mean SD (n)*	*mean SD (n)*
Density	Island	12.6 15.1 (12)	33.3 58.9 (8)	4.8 6.2 (5)	11.6 12.5 (7)	19.0 20.8 (2)
(n/m^2)	West	1.3 1.8 (2)	0.5 0.9 (3)	0 0 (4)	0.04 0.05 (6)	0.1 0.2 (8)
	North	- - (0)	- - (0)	- - (0)	0.3 0.4 (2)	0.02 0.03 (3)
	East	- - (0)	4.0 5.0 (6)	2.9 1.9 (8)	12.3 26.9 (19)	9.0 11.2 (13)
	South	12.3 8.1 (5)	11.1 14.2 (5)	0.2 0.3 (2)	13.8 23.4 (3)	27.3 21.0 (4)
	All flats	9.2 8.65 (7)	5.8 9.5 (14)	1.7 2.1 (14)	9.2 22.8 (30)	8.1 13.6 (28)
Biomass	Island	4.57 4.27	7.67 10.60	1.32 1.84	3.57 3.51	4.14 4.39
($gAFDM/m^2$)	West	0.40 0.53	0.03 0.03	0 0	0 0	0.05 0.09
	North	- -	- -	- -	0.03 0.05	0.01 0.01
	East	- -	3.53 4.42	2.76 1.94	3.34 4.58	4.08 4.58
	South	1.90 1.46	2.37 3.13	0.03 0.04	1.60 2.76	3.05 2.06
	All flats	1.47 1.42	2.36 3.53	1.58 2.01	2.28 3.97	2.34 3.67

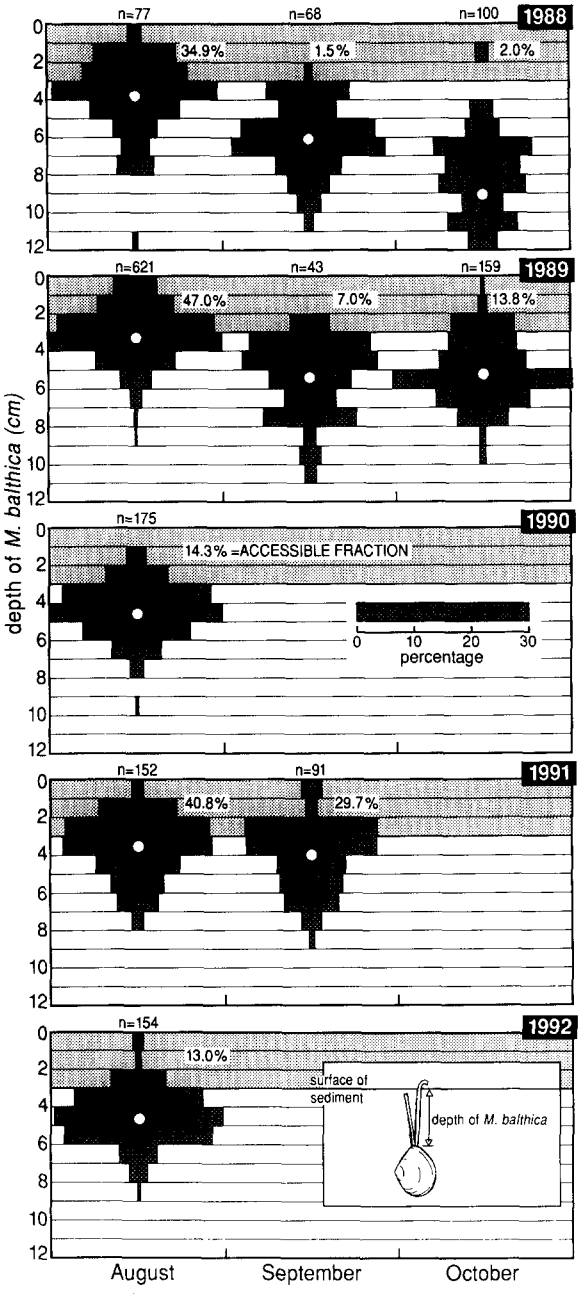


Fig. 17. Seasonal changes in the average depth of suitably sized (3-18 mm long) *Macoma balthica* on the intertidal flats around Griend.

5. DISCUSSION

5.1. USE OF ROOSTING SITES

Why did foraging knots avoid the proximity of the island, and why, from mid-August onwards, did knots only roost on the extensive open flats remaining available east-northeast of Griend at low high-tide levels, flying onto Richel otherwise (Fig. 7)? We suggest that both phenomena have to do with the knots' avoidance of situations where they can be aerially attacked by surprise. This type of hunting is one of the techniques most frequently used by peregrines and merlins. The falcon selects a potential prey from a distance and flies towards its unsuspecting victim at low level, hugging the contours of the landscape (BIJLSMA, 1990; BIJLSMA *et al.*, 1993). Griend with its densely vegetated central area and high dike provides good cover for this kind of attack. Raptor predation has been shown to be an important mortality factor for shorebirds at several sites (*e.g.* PAGE & WHITACRE, 1975; WHITFIELD, 1985), whereas CRESSWELL (1993) shows the importance of flocking behaviour and the avoidance of situations where predatory birds have a chance of surprise attacks. As long as knots remain in the open and in very large flocks (Fig. 20), approaching raptors are likely to be discovered, and the chance for an individual to be attacked and captured must be small. Richel provides an unobstructed view of the horizon and has no structures for raptors to hide in. Although predator abundance has not been measured there, the probability of a successful surprise attack must be one of the lowest in the western Wadden Sea. The reluctance of knots to roost on Griend from mid-August onwards may, therefore, reflect the presence of raptors on the island.

If this hypothesis was true, the daily time and energy expenditure on the extra flights to Richel may

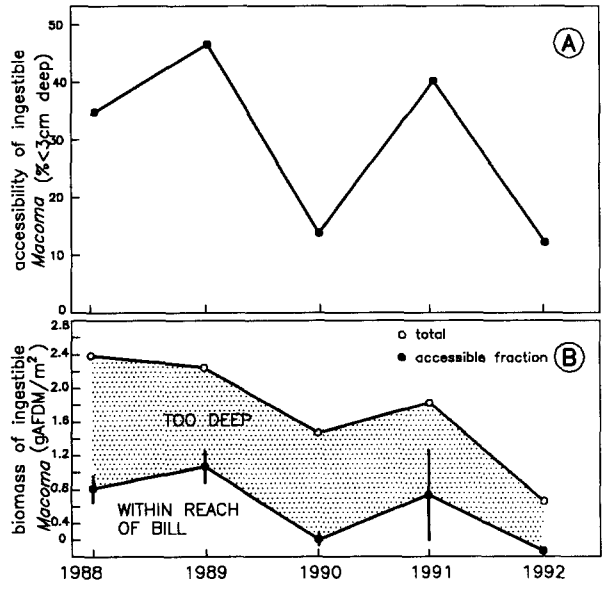


Fig. 18. Yearly variation in the accessibility in August of 3-18 mm long *Macoma balthica* around the island of Griend (A) and how this combines to a picture of the overall change in the biomass availability of *Macoma* in the course of the study period 1988-1992 (B).

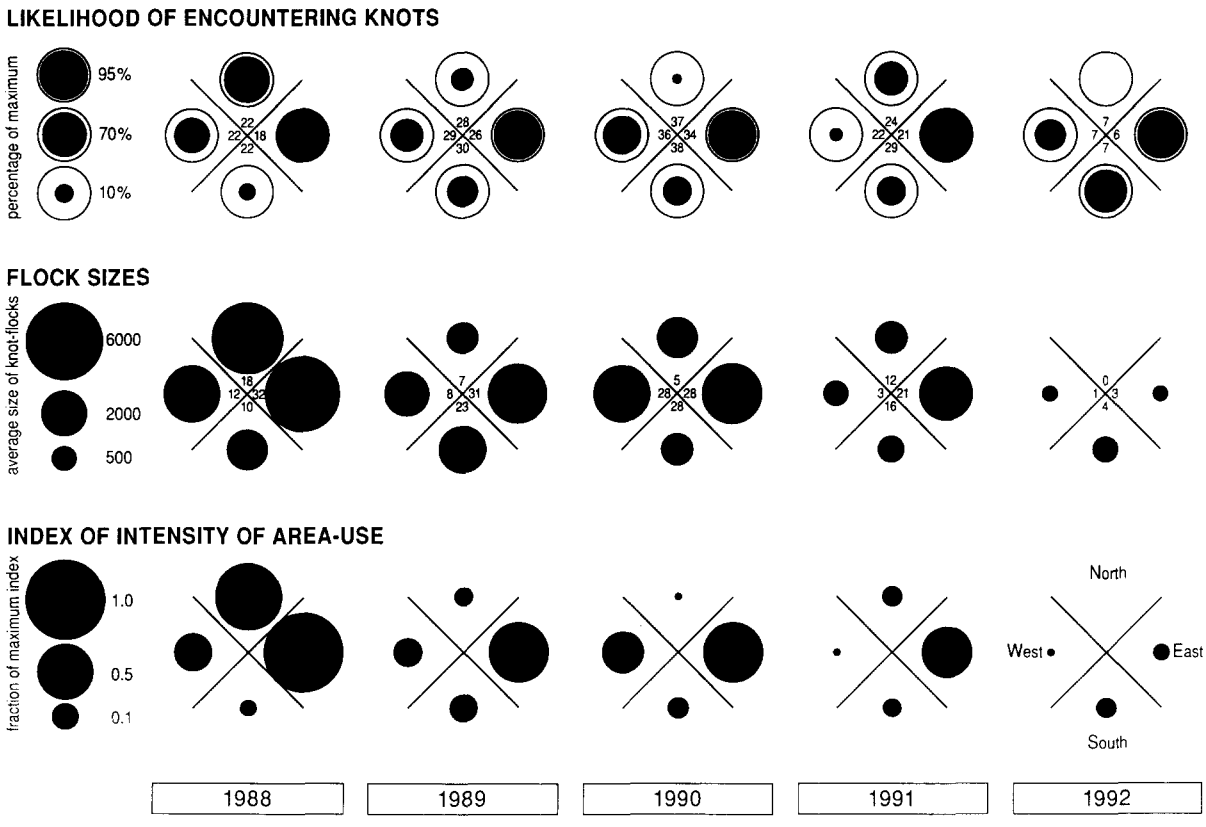


Fig. 19. Coarse-grained distribution patterns of knots over the intertidal flats around Griend. The top row presents the likelihood of encountering knot flocks in the four different sectors (west, north, east and south; see Fig. 2C) in the period August-October 1988-1992 based on systematic surveys of parts of each area on the indicated number of low-water periods. The middle row presents the spatial and yearly variation in the average size of knot flocks encountered on the intertidal flats around Griend in August-October 1988-1992. There were no trends within seasons, but limited sample sizes (number of flocks indicated) and the wide variety of flock sizes encountered (Fig. 20) might have prevented detection of seasonal trends. The bottom row gives indices of the intensity of use of the four sectors around Griend in August-October 1988-1992. We have calculated an index of area-use by multiplying the average encountered flock size in different areas and years (middle row) by the incidence of occurrence of flock sizes of any size in the different areas (top row). The size of the blobs was scaled to the maximum index of area use as in the eastern sector in 1988.

give an indication how much the avoidance of risky situations is valued by knots (*cf.* ABRAHAMS & DILL, 1989; LINDSTRÖM, 1990). With an average of 1.97 high-tides per day, and a one-way distance of 7.5 km between the east point of Griend and Richel, the extra daily flight distance would be 1.97·7.5·2=29.6 km. For a 150-g knot with a wingspan of 0.52 m (see GUDMUNDSSON *et al.*, 1991), PENNYCUICK's (1989) programme predicts a fat consumption at maximum range flight speed (12.3 $m \cdot s^{-1}$) of 0.0272 $g \cdot km^{-1}$. The roosting flight would thus cost 29.6·0.0272=0.81 g fat per day. At 40 kJ per g fat, this would be 0.81·40=32 kJ or *ca* 10% of an approximate daily energy expenditure of 300 kJ per day. The extra daily flight time at the maximum range speed of 12.3 $m \cdot s^{-1}$ (or 44 $km \cdot h^{-1}$) would be 29.6/44=0.67 h, or 2.8% of the time in a day. Of course there may be other reasons than safety to go to Richel at high tide. The coming-together of knot flocks from all over the western Wadden Sea on Richel (A. Koolhaas, A. Dekinga & T. Piersma, in prep.) may allow the gain of information about feeding conditions in other areas, an idea put forward by WARD & ZAHAVI (1973) to explain communal roost and colonial breeding, but which has proven rather difficult to test (DE GROOT, 1980; MOCK *et al.*, 1988).

Raptor predation itself does not explain why curlews and grey plovers (of which the first species, due to its rather larger size, is pretty much immune to raptor predation; WHITFIELD, 1985) usually fly on to Richel during flood as well. Nor does it explain why dunlins *Calidris alpina* (a favoured falcon prey: BIJLSMA, 1990)

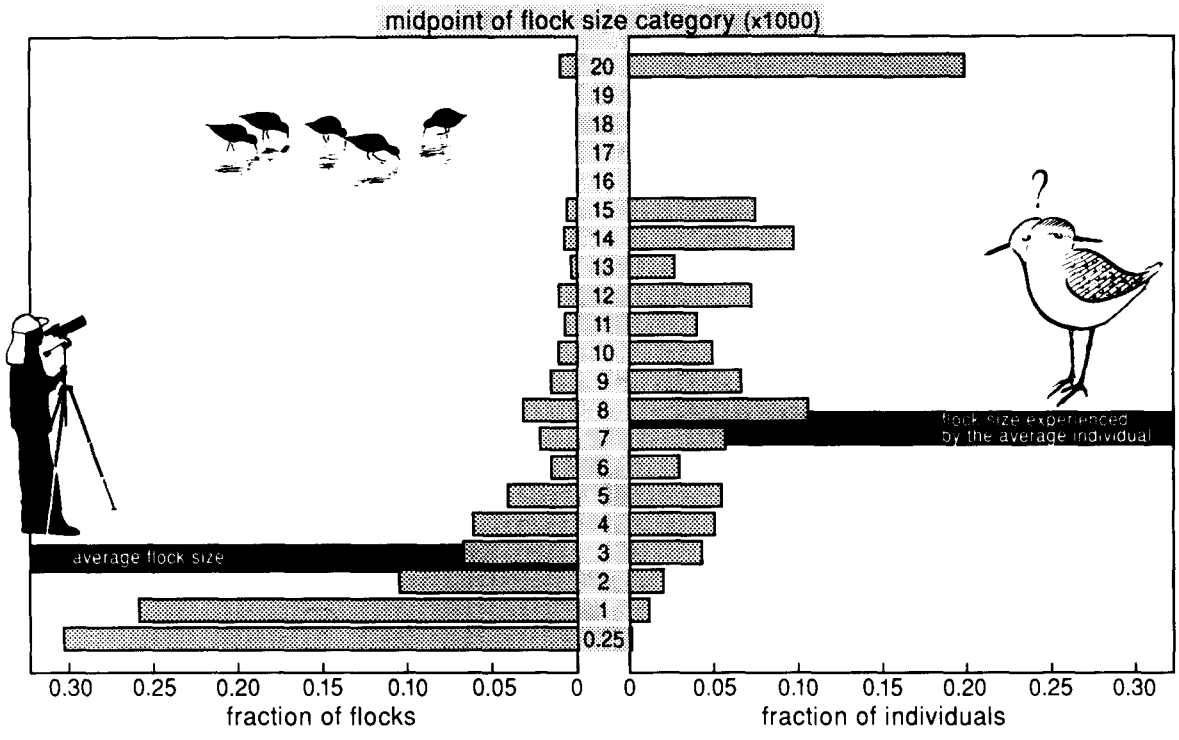


Fig. 20. Frequency distribution of the size of knot flocks encountered on the intertidal flats around Griend in the period August-October 1988-1992. We present both the relative frequency of different flock sizes (on the left side of the y-axis), and the relative frequency of birds as they find themselves in flocks of different size (right side; see JARMAN, 1982 and PIERSMA *et al.*, 1990 for suggesting the difference and an application, respectively). The averages of both measures of flock size are presented as horizontal bars.

remain on Griend to roost in the sheltered saltmarsh in the centre of the island, thereby exposing themselves to surprise attacks. Perhaps the extra flight cost to and from Richel weighs too heavily in the daily energy budget of this small shorebird species, or the energy gain of roosting in the sheltered habitat on Griend relative to the exposed habitat on Richel (HANDEL & GILL, 1992; WIERSMA & PIERSMA, 1994) does not outweigh the reduced predation risk on Richel.

5.2. DIET COMPOSITION

The variable composition of the diet of knots (Fig. 9) reflects to a large extent the availability of the four mollusc prey species. Small *Mytilus* were only available in a few patches in 1992, and hence were only eaten then. *Cerastoderma* of suitable sizes were scarce in 1988 and 1989 (Table 3). In these years *Macoma* was eaten when still present close to the surface in August, being replaced by *Hydrobia* later in the season. *Hydrobia* always occurred in good densities east of the island (Table 4), but was the least popular prey species. *Hydrobia* was only fed upon when neither *Macoma*, *Cerastoderma* nor *Mytilus* were available in profitable (harvestable) densities. The avoidance of *Hydrobia* is easily explained by their low profitability. Even at the highest densities, the biomass of ingested *Hydrobia* per unit handling time is never more than 0.9 mg AFDM·s^{-1} (this is due to their low individual biomass in relation to handling time), whereas the other prey species have profitabilities over 1 mg AFDM·s^{-1} at much lower harvestable biomass densities (T. Piersma & J. van Gils, in prep.).

Macoma was, therefore, the preferred prey, and their contribution to the diet of knots is a nice threshold function of their harvestable biomass, even if averaged per sector and time period (Fig. 21). At harvestable biomass densities over 0.8 to 1 g AFDM per m^2, *Macoma* made up most of the ingested biomass. Similar density thresholds have been reported for knots feeding in the Dutch and German Wadden Sea in spring (T. Piersma, Y. Verkuil & I Tulp, in prep.). The general preference for *Macoma* in the Wadden Sea (ZWARTS & BLOMERT, 1992; this study) must be due to their high profitability (T. Piersma, J. van Gils & P. de Goeij, in prep.), combined with their thin shells and low shell/meat ratios compared to *Cerastoderma* (ZWARTS & BLOMERT, 1992).

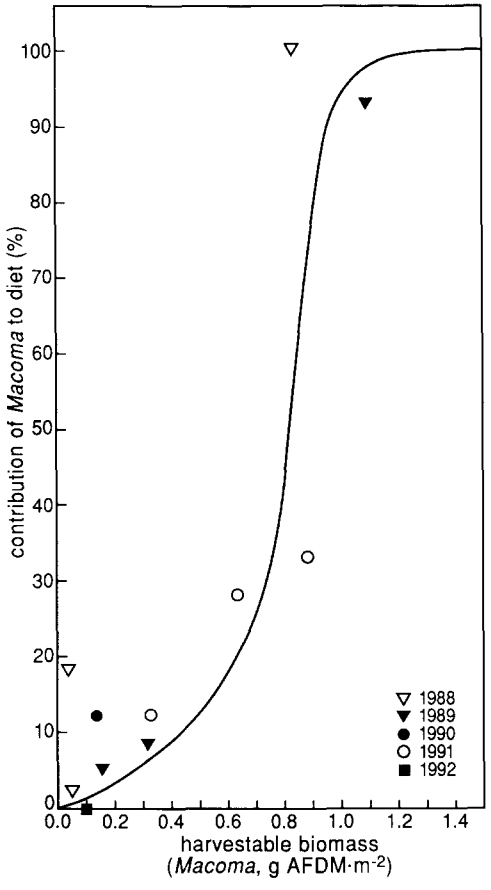


Fig. 21. Contribution of *Macoma balthica* to the diet of knots near Griend in 1988-1992 as a function of the overall harvestable biomass of *Macoma*. The percentages *Macoma* in diet in different (half-)monthly periods were taken from Fig. 9, and the harvestable biomass computed by multiplying the biomass of the suitable size classes in different years (Table 2) with the percentage accessible (Fig. 17). The line helps the eye to see the threshold function.

5.3. CORRELATING FOOD WITH NUMBERS OF FEEDING KNOTS

Do knots distribute themselves over the flats around the island according to the distributions of their food, or is our description of their diet and of food abundance still inadequate to explain the patterns over a rather large scale? In view of their variable diet, we have plotted the area use by knots of different sectors around the island in different years (Fig. 19, bottom row) as a function of the early-season harvestable biomass of the most commonly eaten prey at that time, *i.e. Macoma* in 1988 and 1989 and *Cerastoderma* in the three remaining years (Fig. 22). In four out of the five years the rank correlations are 1; only in 1989 was the western sector less used than predicted if the presence of knots is indeed ranked to the abundance of *Cerastoderma*. The size and frequency of occurrence of knot flocks are therefore clear functions of food abundance, which was also found by ZWARTS *et al.* (1992) for knots along the Frisian mainland coast.

However, the (*canutus*-) knots along the Frisian mainland coast studied by ZWARTS *et al.* (1990) only visited their study area to feed on *Macoma* when the harvestable biomass of *Macoma* was as large as 4 g AFDM per m^2, rather than 0.8 g AFDM per m^2 as reported here (*cf.* Figs 21 and 22). Since we now know that knots can make a living at harvestable *Macoma*-biomass values of about 1 g AFDM per m^2 (T. Piersma, Y. Verkuil, I. Tulp, J. van Gils & P. de Goeij, in prep.), the reason for not visiting the Frisian foreshore at harvestable biomass densities, which are still much higher than those in the western Wadden Sea, must involve factors other than food abundance (note that the smaller resolution of the observations by ZWARTS *et al.* (1992) compared to our study would automatically lead to a somewhat higher threshold since our coarse-scale biomass figures would be biased downwards by the inclusion of barren spots not visited by knots to a greater extent than Zwarts'). There is a possibility that the avoidance of obstructions in the landscape such as the high dike along the coast of Friesland, a feature which can hide approaching predators, or provide an entry for other disturbing factors such as human activity (PFISTER *et al.*, 1992), may be involved, even though the knots usually remained at least 0.5 km from the dike. Breeding origin may also play a role since *canutus*–knots regularly roosted on the saltmarsh of Griend in contrast with the later occurring *islandica*-knots. Yet another possibility is that knots make a trade-off between the costs of foraging and food abundance. The Frisian foreshore combines a rather soft and silty substrate (and potentially high walking costs) with a lot of food. More data of the kind presented here and by ZWARTS *et al.* (1990) need to be assembled for stronger inferences about these issues.

5.4. SPACE USE BY KNOTS

In our attempts to explain the low- and high-water distributions of knots in the Wadden Sea, we have been riding the familiar horses of profitability of feeding grounds and probability of predatory attacks (*e.g.* GUILLEMETTE *et al.*, 1993). Yet, there is one striking aspect of the distribution of knots for which additional explanations need to be sought, perhaps in a different but still comparative way. As is indicated by the large day-to-day fluctuations in the numbers of knots seen around Griend (Fig. 5) and illustrated in Fig. 1, individual knots roam over enormous areas in the course of a couple of tidal cycles. This confirms earlier findings by PRATER (1972) in Morecambe Bay and by SYMONDS *et al.* (1984) in the Firth of Forth, both in the

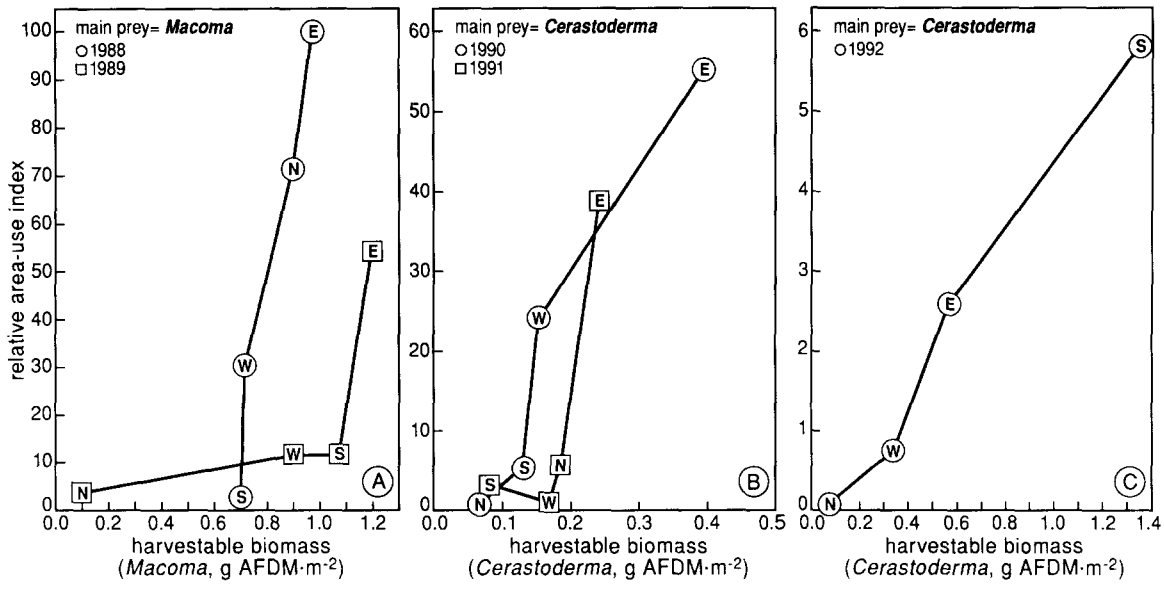


Fig. 22. Numerical responses of knots on the intertidal areas around Griend in 1988-1992. For each year the indices of intensity of area use (see Fig. 19) of the four different sectors around Griend are plotted as a function of the harvestable biomass in that sector of the most commonly eaten prey in that year (*Macoma* in 1988 and 1989, panel A; *Cerastoderma* in the remaining three years, panels B and C). The intensities of area use were scaled to the maximum index of area use (100) as in the eastern sector in 1988. Since numbers of knots were very low in 1992, a separate panel (C) presents the data for that year.

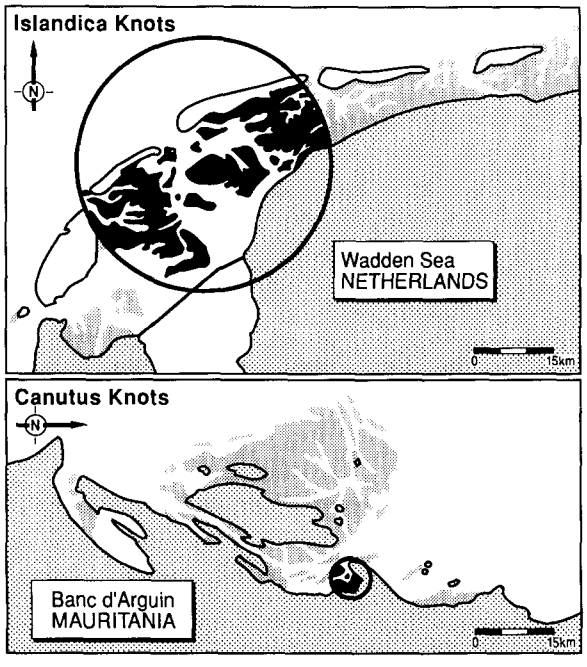


Fig. 23. Approximate use of space by knots in the Wadden Sea, The Netherlands (A) and on the Banc d'Arguin, Mauritania (B). These maps are based on unpublished information of A. Koolhaas, J. van Gils, A. Dekinga, M. Kersten & T. Piersma. The two maps are to scale.

British Isles. Based on our work in 1988-1992 and more detailed studies in July-September 1993 (A. Koolhaas, J. van Gils, T. Piersma & A. Dekinga, in prep.), we have tried to estimate the total area of intertidal flats and channels ranged over by knots in a couple of tides (Fig. 23A). During this period, Knots used an area with a diameter of 45-50 km, covering as much as an estimated 800 km^2 of tidal habitat.

This is in stark contrast with the situation at another important moulting and wintering area for knots, the Banc d'Arguin in Mauritania (ALTENBURG *et al.*, 1982), where studies in spring 1985 and 1988 have shown them to use much smaller areas (Fig. 23B). In the course of March-April 1985, colour-marked knots remained within a radius of 3 km of their roosting sites (where they were also captured), thus covering an estimated 10-15 km^2 of tidal habitat (M. Kersten & T. Piersma, unpubl. data). One major difference between the western Wadden Sea and intertidal areas in West Africa is that knots are likely to feed on a larger number of different prey species in Africa, 10-15 species rather than 4 (T. Piersma, in prep.). A diverse diet composed of several prey species with non-synchronous biomass fluctuations which generally live rather close to the sediment surface (PIERSMA *et al.*, 1993b) makes up for rather more or less constant feeding conditions in West Africa. Tropically wintering knots may not have to roam around in large flocks to the extent that they do in the western Wadden Sea in order to keep track of the ever changing

feeding conditions due to vertical movements of prey in the sediment and other environmental perturbations such as human shell-fishing activities. More descriptive studies under different diet and prey availability regimes, possibly involving the radio-tracking of individual knots over feeding areas in combination with detailed diet, energy-intake, and food-availability studies, are called for to test these hypotheses.

6. CONCLUSIONS

In the western Wadden Sea, knots can range widely in the course of a couple of tidal cycles, probably covering as much as 800 km^2. In addition, they usually fly an extra 30 km per day to get to what must be the preferred roost site, accepting an increase of the daily energy expenditure of about 10%. The number of knots using the intertidal flats around Griend for feeding has decreased between 1988 and 1992, and this decrease parallels the decrease in the stocks of *Macoma*. *Macoma* is the major prey type when their harvestable biomass (averaged over large areas) is larger than 0.8 g AFDM per m^2, the birds switching to a diet of juvenile *Cerastoderma* if *Macoma* are too sparse, and to *Hydrobia* if both *Macoma* and *Cerastoderma* are scarce. In a comparison between areas and years, the use of different sectors around the island by knots is best explained by the abundance of the prevalent prey species. The intertidal area close to the island is avoided, perhaps to reduce the probability of being taken by surprise by a raptor. Although the correlative nature of a descriptive study like this does not allow us to firmly establish thresholds in food density determining occurrence, it does give strong suggestions as to the factors that matter to knots when they choose their feeding and roosting sites. It also suggests the large extent of intertidal area over which knots, in flocks of 4000 to 15000 birds, vary feeding locations from day to day.

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As we go into print we learned about the sudden death of Kees de Boer from West-Terschelling. A warm personality and a true friend of Griend, its wildlife and its temporary inhabitants is lost much too early. We dedicate this paper to his memory.

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APPENDIX

Estimation of diet composition in biomass terms on the basis of droppings.

The species-specific contributions of the dry mass of shell material retained on 300-μm sieves (partial-DM_{drop}) was used to either estimate the dry shell mass (DM_{shell}, in the three bivalve species) or the total ash mass (DM_{ash}, in the mudsnail *Hydrobia*) on the basis of the equations presented by DEKINGA & PIERSMA (1993: table 1). DM_{shell} and DM_{ash} were then multiplied by the appropriate DM/AFDM-ratios to estimate the AFDM-contribution. For the three common prey we have examined whether there was size-, and year-specific variation in these ratios, as recommended by DEKINGA & PIERSMA (1993).

Macoma balthica.—DM_{shell} was estimated from partial-DM_{drop} by multiplying with 0.994. Then the biomass contributed by *Macoma* was predicted from DM_{shell}, by multiplying with the appropriate $AFDM_{shell}/DM_{shell}$ ratio. An analysis of covariance of ratio-values from August-October with length as the covariate showed that the $AFDM_{meat}/DM_{shell}$-ratios were significantly different both with respect to year ($F=9.27$, $p<0.001$, $n=607$) as with respect to shell length ($F=453.78$, $p<0.001$). To alleviate the effect of outlying average $AFDM_{meat}/DM_{shell}$-ratios, which were usually due to small sample sizes, we estimated the log-log regressions of $AFDM_{meat}/DM_{shell}$ (dimensionless) on shell length (SL, in mm) for the four years (1989-1992) that we have data. For 1989, $AFDM_{meat}/DM_{shell} = 1.976 \cdot SL^{-1.057}$ ($r^2=0.98$, $n=216$); for 1990, $AFDM_{meat}/DM_{shell} = 3.763 \cdot SL^{-1.264}$ ($r^2=0.80$, $n=27$); for 1991, $AFDM_{meat}/DM_{shell} = 0.630 \cdot SL^{-0.604}$ ($r^2=0.48$, $n=188$); for 1992, $AFDM_{meat}/DM_{shell} = 0.681 \cdot SL^{-0.648}$ ($r^2=0.91$, $n=177$). For 1988 we used the overall average shell length-dependent ratios as computed from the above data sets.

Cerastoderma edule.—DM_{shell} was estimated from partial-DM_{drop} by multiplying with 0.994. Then the biomass contributed by *Cerastoderma* was predicted from DM_{shell}, by multiplying with the appropriate $AFDM_{shell}/DM_{shell}$ ratio. An analysis of covariance of ratio-values from August-October with length as the covariate showed that the $AFDM_{meat}/DM_{shell}$-ratios were significantly different both with respect to year ($F=35.43$, $p<0.001$, $n=307$) as with respect to shell length ($F=18.58$, $p<0.001$). To alleviate the effect of outlying average $AFDM_{meat}/DM_{shell}$-ratios, we estimated the log-log regressions of $AFDM_{meat}/DM_{shell}$ (dimensionless) on shell length (SL, in mm) for the four years (1989-1992) that we have data. For 1989, $AFDM_{meat}/DM_{shell} = 0.130 \cdot SL^{-0.353}$ ($r^2=0.49$, $n=54$); for 1990, $AFDM_{meat}/DM_{shell} = 0.249 \cdot SL^{-0.519}$ ($r^2=0.16$, $n=13$); for 1991, $AFDM_{meat}/DM_{shell} = 0.084 \cdot SL^{-0.109}$ ($r^2=0.15$, $n=117$); for 1992, $AFDM_{meat}/DM_{shell} = 0.130 \cdot SL^{-0.214}$ ($r^2=0.32$, $n=124$). For 1988 we used the overall average shell length-dependent ratios as computed from the above data sets.

Hydrobia ulvae.—DM_{ash} was estimated from partial-DM_{drop} by multiplying with 1.267 (DEKINGA & PIERSMA 1993: table 1). Then the biomass contributed by *Hydrobia* was predicted from DM_{ash}, by multiplying with the $AFDM_{total}/DM_{ash}$ ratio. For all data from August-October, there was no relationship between the $AFDM_{total}/DM_{ash}$-ratio and shell length (oneway ANOVA, $F=1.23$, $p=0.28$, $n=374$), but there existed significant variation between years (oneway ANOVA, $F=13.0$, $p<0.0001$) (we performed two ANOVA's in succession since there was little year-bias in the contribution of different length-categories). The length-independent ratios for the different year are as follows. 1988: 0.170 (SD=0.030, number of samples=37); 1989: 0.177 (0.039, 65); 1990: 0.165 (0.026, 63); 1991: 0.187 (0.043, 96); 1992: 0.153 (0.030, 113); with the overall average over 374 samples from Griend being 0.170.